MOLECULAR PHYLOGENETIC ANALYSIS OF THE AMERICAN STIPEAE (POACEAE) RESOLVES *JARAVA* SENSU LATO POLYPHYLETIC: EVIDENCE FOR A NEW GENUS, *PAPPOSTIPA*

Konstantyn Romaschenko

M.G. Kholodny
Institute of Botany
National Academy of Sciences of Ukraine
01601 Kiev, UKRAINE
kromaschenko@gmail.com

Paul M. Peterson and Robert J. Soreng

Department of Botany
National Museum of Natural History
Smithsonian Institution
Washington, DC 20013-7012, U.S.A.
peterson@si.edu; sorengr@si.edu

Nuria Garcia-Jacas

Laboratory of Molecular Analysis
Botanic Institute of Barcelona (CSIC-ICUB)
Pg. del Migdia, s. n.
08038 Barcelona, SPAIN
ngarciajacas@ibb.csic.es

Oksana Futorna

M.G. Kholodny Institute of Botany
National Academy of Sciences of Ukraine
01601 Kiev, UKRAINE
oksana_drofa@yahoo.com

Alfonso Susanna

Botanic Institute of Barcelona (CSIC-ICUB)
Pg. del Migdia, s. n.
08038 Barcelona, SPAIN
asusanna@ibb.csic.es

ABSTRACT

A molecular phylogenetic analysis based on plastid (*trn*K-*mat*K, *mat*K, *trn*H-*psb*A, and *trn*L-*trn*F regions) and nuclear ITS DNA sequences of 68 species representing 11 genera suggests an entirely new hypothesis for the evolutionary history within the tribe. *Piptochaetium*, *Anatherostipa*, *Ptilagrostis* and *Hesperostipa* are basal lineages that diverge independently from a clade that includes a monophyletic *Jarava* subg. *Pappostipa* (rendering *Jarava* s.l. polyphyletic) that is sister group to *Austrostipa* plus a subclade referred to as the "Major American Clade" (MAC). Within the MAC, New World *Achnatherum* is the sister group of a grade or clade of *Jarava* s.s. and a *Nassella-Amelichloa* clade. *Jarava* subg. *Pappostipa* is monophyletic and not closely related to other sampled species of *Jarava*, supporting recognition of the new genus **Pappostipa** (Speg.) Romaschenko, P.M. Peterson & Soreng with 23 species; *Stipa speciosa* selected as the lectotype. Within *Pappostipa* we identify two clades that we recognize as new sections, and we make new combinations to transfer *Jarava* subsp. *Pappostipa* species to the new genus: *Pappostipa* sect. **Chrysovaginatae** Romaschenko, with the following new combinations: **Pappostipa sorianoi** (Parodi) Romaschenko, **Pappostipa atacamensis** (Parodi) Romaschenko, **Pappostipa nana** (Speg.) Romaschenko, **Pappostipa ibarii** (Phil.) Romaschenko, **Pappostipa ibarii** f. **pallescens** (Parodi) Romaschenko, **Pappostipa ibarii** var. **anomala** (Parodi) Romaschenko, **Pappostipa ameghinoi** (Speg.) Romaschenko, **Pappostipa ameghinoi** var. **digona** (Parodi) Romaschenko, **Pappostipa ameghinoi** var. **precordillerana** (F.A. Roig) Romaschenko, **Pappostipa chubutensis** (Speg.) Romaschenko, **Pappostipa chubutensis** var. **hirsutissima** (F.A. Roig) Romaschenko, **Pappostipa frigida** (Phil.) Romaschenko, **Pappostipa frigida** var. **parvispicula** (Parodi) Romaschenko, **Pappostipa humilis** (Cav.) Romaschenko, **Pappostipa humilis** var. **decrescens** (Kuntze) Romaschenko, **Pappostipa humilis** var. **ruiziana** (Parodi) Romaschenko, **Pappostipa chrysophylla** (E. Desv.) Romaschenko, **Pappostipa chrysophylla** f. **minuta** (F.A. Roig) Romaschenko, **Pappostipa chrysophylla** var. **cordillerarum** (Parodi) Romaschenko, **Pappostipa chrysophylla** var. **crispula** (Kuntze) Romaschenko, and **Pappostipa chrysophylla** f. **modica** (F.A. Roig) Romaschenko. *Pappostipa* sect. **Pappostipa** includes the following new combinations: **Pappostipa speciosa** (Trin. & Rupr.) Romaschenko, **Pappostipa speciosa** var. **manqueclensis** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **atuelensis** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **parva** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **breviglumis** (Parodi) Romaschenko, **Pappostipa speciosa** var. **ciliata** (F.A. Roig) Romaschenko, **Pappostipa speciosa** f. **horrida** (F.A. Roig) Romaschenko, **Pappostipa speciosa** f. **abscondita** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **media** (Torres) Romaschenko, **Pappostipa vaginata** (Phil.) Romaschenko, **Pappostipa vaginata** f. **rigida** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **inmersa** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **laevis** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **contracta** (F.A. Roig) Romaschenko, **Pappostipa vaginata** var. **argyroidea** (F.A. Roig) Romaschenko, **Pappostipa vaginata** var. **dilatata** (F.A. Roig) Romaschenko, **Pappostipa nicorae** (F.A. Roig) Romaschenko, **Pappostipa hieronymusii** (Pilg.) Romaschenko, **Pappostipa patagonica** (Speg.) Romaschenko, **Pappostipa maeviae** (F.A. Roig) Romaschenko,

Pappostipa parodiana (F.A. Roig) Romaschenko, **Pappostipa braun-blanquetii** (F.A. Roig) Romaschenko, **Pappostipa semperiana** (F.A. Roig) Romaschenko, **Pappostipa ruiz-lealii** (F.A. Roig) Romaschenko, **Pappostipa malalhuensis** (F.A. Roig) Romaschenko, **Pappostipa major** (Speg.) Romaschenko, **Pappostipa vatroensis** (F.A. Roig) Romaschenko, and **Pappostipa barrancaensis** (F.A. Roig) Romaschenko.

RESUMEN

Un análisis filogenético basado en los datos moleculares de varías regiones plastidiales (*trn*K-*mat*K, *mat*K, *trn*H-*psb*A y *trn*L-*trn*F), y las secuencias nucleares del ITS de 68 especies representando 11 géneros, resulta en una nueva hipótesis de la historia evolutiva de la tribu. El conjunto de los *Piptochaetium*, *Anatherostipa*, y *Ptilagrostis* (con *Hesperostipa* como un clado adyacente) se presenta como un linaje basal que diverge independientemente del clado monofiletico que incluye *Jarava* subg. *Pappostipa* (lo que hace *Jarava* s.l. polifilético) que es, a su vez, un grupo hermano para *Austrostipa* y un subclado al que nos como "clado americano mayor" (MAC). Dentro del MAC el *Achnatherum* del Nuevo Mundo se presenta como un grupo hermano para un complejo formado por los clados de *Jarava* s.s. y *Nassella* con el género *Amelichloa* incloido. El hecho de que *Jarava* subg. *Pappostipa* sea monofiletico y no se relacione con el resto del *Jarava* s.l. apoya la separación del *Pappostipa* (Speg.) Romaschenko, P.M. Peterson & Soreng como un genero nuevo con 23 especies; *Stipa speciosa* seleccionado como el lectotipo. Dentro del *Pappostipa* las dos secciones fueron reconocidas basando sobre los datos moleculares y morfológicos. Para la transferencia del *Jarava* subsp. *Pappostipa* a un género nuevo se proponen las necesarias combinaciones taxonómicas apropiadas: *Pappostipa* secc. **Chrysovaginatae** Romaschenko, con las siguientes combinaciones nuevas: **Pappostipa sorianoi** (Parodi) Romaschenko, **Pappostipa atacamensis** (Parodi) Romaschenko, **Pappostipa nana** (Speg.) Romaschenko, **Pappostipa ibarii** (Phil.) Romaschenko, **Pappostipa ibarii** f. **pallescens** (Parodi) Romaschenko, **Pappostipa ibarii** var. **anomala** (Parodi) Romaschenko, **Pappostipa ameghinoi** (Speg.) Romaschenko, **Pappostipa ameghinoi** var. **digona** (Parodi) Romaschenko, **Pappostipa ameghinoi** var. **precordillerana** (F.A. Roig) Romaschenko, **Pappostipa chubutensis** (Speg.) Romaschenko, **Pappostipa chubutensis** var. **hirsutissima** (F.A. Roig) Romaschenko, **Pappostipa frigida** (Phil.) Romaschenko, **Pappostipa frigida** var. **parvispicula** (Parodi) Romaschenko, **Pappostipa humilis** (Cav.) Romaschenko, **Pappostipa humilis** var. **decrescens** (Kuntze) Romaschenko, **Pappostipa humilis** var. **ruiziana** (Parodi) Romaschenko, **Pappostipa chrysophylla** (E. Desv.) Romaschenko, **Pappostipa chrysophylla** f. **minuta** (F.A. Roig) Romaschenko, **Pappostipa chrysophylla** var. **cordillerarum** (Parodi) Romaschenko, **Pappostipa chrysophylla** var. **crispula** (Kuntze) Romaschenko, and **Pappostipa chrysophylla** f. **modica** (F.A. Roig) Romaschenko. Dentrode *Pappostipa* secc. **Pappostipa** proponemos las nuevas combinaciones siguientes: **Pappostipa speciosa** (Trin. & Rupr.) Romaschenko, **Pappostipa speciosa** var. **manqueclensis** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **atuelensis** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **parva** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **breviglumis** (Parodi) Romaschenko, **Pappostipa speciosa** var. **ciliata** (F.A. Roig) Romaschenko, **Pappostipa speciosa** f. **horrida** (F.A. Roig) Romaschenko, **Pappostipa speciosa** f. **abscondita** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **media** (Torres) Romaschenko, **Pappostipa vaginata** (Phil.) Romaschenko, **Pappostipa vaginata** f. **rigida** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **inmersa** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **laevis** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **contracta** (F.A. Roig) Romaschenko, **Pappostipa vaginata** var. **argyroidea** (F.A. Roig) Romaschenko, **Pappostipa vaginata** var. **dilatata** (F.A. Roig) Romaschenko, **Pappostipa nicorae** (F.A. Roig) Romaschenko, **Pappostipa hieronymusii** (Pilg.) Romaschenko, **Pappostipa patagonica** (Speg.) Romaschenko, **Pappostipa maeviae** (F.A. Roig) Romaschenko, **Pappostipa parodiana** (F.A. Roig) Romaschenko, **Pappostipa braun-blanquetii** (F.A. Roig) Romaschenko, **Pappostipa semperiana** (F.A. Roig) Romaschenko, **Pappostipa ruiz-lealii** (F.A. Roig) Romaschenko, **Pappostipa malalhuensis** (F.A. Roig) Romaschenko, **Pappostipa major** (Speg.) Romaschenko, **Pappostipa vatroensis** (F.A. Roig) Romaschenko y **Pappostipa barrancaensis** (F.A. Roig) Romaschenko.

The tribe Stipeae Dumort. are temperate, cool-season (C_3) grasses that generally occupy somewhat moist to predominantly dry open grasslands and steppe communities in all continents except Antarctica. Worldwide the Stipeae consist of a minimum of 21 genera and 524–604 species, depending on how Asian taxa are recognized (Soreng & Davis 2005). In the New World there are 279 species of Stipeae (Soreng et al. 2008); of these, 222 (79.6%) are found in South America. Thirteen genera are indigenous, and nine are endemic to the New World. The Stipeae s.s. (excluding elements of Phaenospermateae Renvoize & Clayton, and subtribes Ampelodesminae Connert and Duthieinae Pilg. ex Potztal) are characterized by having single-flowered spikelets with terminally-awned lemmas where the awn is the result of the fusion between the central and two lateral vascular traces, simple starch grains, florets with two or three linear lodicules, and small-sized chromosomes with a base number of x = 10–12. The Stipeae are placed in subfamily Pooideae (GPWG 2001). Within the Pooideae they are an 'early diverging' lineage that arose after the separations of the Brachyelytreae Ohwi, and Lygeeae J. Presl plus Nardeae W.D.J. Koch (Davis & Soreng 2007).

Historically, delimitation of genera within the American Stipeae was based on a broad concept of the genus *Stipa* L. Hitchcock (1935, 1951) accepted three genera in North America: *Oryzopsis* Michx., *Piptochaetium* J. Presl, and *Stipa*. In South American Stipeae, Spegazzini (1901) recognized only *Aciachne* Benth.,

Oryzopsis, and *Stipa*. In the second part of the 20th century, Stipeae taxonomy was characterized by the consecutive resurrection of previously described genera or emendation of taxa considered by Spegazzini (1901, 1925) as subgenera of *Stipa*. *Nassella* (Trin.) E. Desv. was restored to generic status by Parodi (1947) and significantly expanded, and thus became the most species rich genus among American Stipeae (Barkworth 1990; Barkworth & Torres 2001). In considering the distribution of morphological features among stipoid grasses and lemma epidermal features (Thomasson 1978, 1980, 1981, 1982), Barkworth and Everett (1987) suggested that *Stipa* includes only Eurasian species: Hence the name *Stipa* should not be used for any American species. In subsequent major rearrangements of the American Stipeae, five species were transferred to *Hesperostipa* (M.K. Elias) Barkworth. Thirty-seven other American species formerly placed in *Stipa* or *Oryzopsis* were shown to share some morphological features with the Eurasian representatives of *Achnatherum* P. Beauv.; they were transferred to the latter genus (Barkworth 1993). *Stipa* subg. *Anatherostipa* Hack. ex Kuntze (Kuntze 1898; Spegazzini 1901, 1925), including the Obtusae group of Parodi (1946), was recently established at the generic rank by Peñailillo (1996), currently with 11 species (Soreng et al. 2003). *Nassella* now includes 115 and *Piptochaetium* 35 species, respectively (Soreng et al. 2003).

The genus *Jarava* Ruiz et Pav. was resurrected by Rojas (1997), in the sense of *Stipa* subg. *Jarava* (Ruiz et Pav.) Trin. & Rupr. (Caro & Sánchez 1973), and significantly expanded by Peñailillo (2002, 2003) to 55 species by inclusion of *Stipa* subg. *Pappostipa* Speg. and *S.* subg. *Ptilostipa*. Speg. The expansion of *Jarava* effectively completed the removal of all remaining accepted indigenous New World species from the genus *Stipa*, as anticipated by Barkworth and Everett (1987). However, Stipeae taxonomists generally acknowledged that such a broadly circumscribed *Jarava* was probably polyphyletic, and Arriaga and Barkworth (2006) began to revise it by transferring five *Jarava* s.l. species to a new genus, *Amelichloa* Arriaga & Barkworth.

Parodi (1960) recognized two main morphological leaf types in Spegazzini's *Stipa* subg. *Pappostipa*, represented by *Stipa speciosa* and *S. humilis* (Arriaga 1983). The first type (leaf anatomical "type I" of Arriaga 1983) encompassed species with stiff, thick, and usually pungent leaves. The second type ("type II" of Arriaga 1983) covered species with comparatively thin, slender, and non-pungent leaves. Later, Parodi (1960), followed by Roig (1964) and Nicora and Rúgolo de Agrasar (1978), noted that species with the former type had brownish-red basal sheaths and species with the latter type had pale basal sheaths.

There have been several attempts to infer phylogenetic relationships among stipoid genera based on morphological evidence (Tzvelev 1977; Barkworth & Everett 1987; Thomasson 1978, 1985) and preliminary molecular analyses (Jacobs et al. 2000, 2007; Cialdella et al. 2007). The origins of *Hesperostipa*, *Jarava* s.s., *Piptochaetium*, and *Stipa* s.s. have been reported as monophyletic (Jacobs et al. 2000, 2007; Cialdella et al. 2007), but the overall phylogeny of the American Stipeae remains poorly resolved and contradictory.

Our preliminary study of the Stipeae phylogeny based on ITS sequence data (Romaschenko et al. 2007) revealed a deep separation between a Euro-Mediterranean clade, including *Stipa* s.s., and a clade including genera and species of East Asian, Australian, and American origin. In addition, *Jarava* (sensu Peñailillo 2003) was resolved as polyphyletic, with a clade of species formerly placed in *Stipa* subg. *Pappostippa*, clearly independently derived from the core species of *Jarava* s.s.

The main objectives of this paper are to present a phylogenetic hypothesis for the American Stipeae and to evaluate the monophyly of *Jarava* s.l. based on an analyses of plastid (*mat*K, *trn*K-*mat*K, *trn*H-*psb*A and *trn*L-*trn*F) and nuclear ribosomal ITS DNA sequences. We also discuss morphological and anatomical characters that support our phylogenetic inferences.

METHODS

Taxon sampling.—The majority of the specimens sampled in this study were collected by PMP and RJS, and are deposited at the Smithsonian Institution, United States National Herbarium (US). Eighty-one samples representing 66 species and three infraspecific taxa, with duplicates for nine taxa, were included in our analysis (Table 1). These represent eight of the 11 Stipeae genera reported as indigenous for the Americas (Soreng et al. 2003), plus the newer segregate genus, *Amelichloa*. Thirteen species collectively of minor South

TABLE 1. Stipeae species sampled, sources of material, vouchers, and GenBank accession numbers for DNA sequences. Species with an asterisk* now in *Pappostipa*; sequence partially incomplete with a degree ° symbol; [1,2,3] = duplicate specimens sampled.

Taxon	Country	Voucher	trnK-matK	matK	trnH-psbA	trnL-trnF	ITS
Achnatherum aridum (M.E. Jones) Barkworth	USA	*Tiehm & Nachlinger 13518* (US)	EU489382	EU489170	EU489237	EU489311	EU489089
Achnatherum occidentale (Thurb. ex. S. Watson) Barkworth	Canada	*Saarela, Sears & Maze 594* (UBC)	EU489383	EU489171	EU489238	EU489312	EU489090
Achnatherum occidentale subsp. *pubescens* (Vasey) Barkworth	USA	*Soreng 7418* (US)	EU489384	EU489172	EU489239	EU489313	EU489091
Achnatherum parishii (Vasey) Barkworth	USA	*Roos & Roos 4895* (US)	EU489385	–	EU489240	EU489314	EU489092
Achnatherum richardsonii (Link) Barkworth	Canada	*Peterson, Saarela & Smith 18399* (US)	EU489386	EU489173	–	EU489315	EU489093
Amelichloa caudata (Trin.) Arriaga & Barkworth[1]	Argentina	*Pyke 596* (BC)	EU489387	EU489174	–	EU489316	EU489094
Amelichloa caudata (Trin.) Arriaga & Barkworth[2]	Argentina	*Peterson & Annable 11398* (US)	EU489388	EU489175	EU489241	EU489317	EU489095
Amelichloa clandestina (Hack.) Arriaga & Barkworth	Mexico	*Hoge, Barkworth & Carranza 286* (US)	EU489389	–	EU489242	–	EU489096°
Anatherostipa bomanii (Hauman) Peñailillo	Bolivia	*Peterson, Soreng & Romaschenko 20710* (US)	EU489390	EU489176	EU489243	EU489318	EU489097
Anatherostipa hans-meyeri (Pilg.) Peñailillo	Peru	*Peterson, Soreng & Romaschenko 20645* (US)	EU489391	EU489177	EU489244	EU489319	EU489098
Anatherostipa rigidiseta (Pilg.) Peñailillo	Peru	*Peterson, Soreng & Romaschenko 20724* (US)	EU489392	EU489178	EU489245	EU489320	EU489099
Austrostipa compressa (R.Brown) S.W.L. Jacobs & J. Everett	Australia	*Peterson, Soreng & Rosenberg 14514* (US)	EU489393	EU489179	EU489246	EU489321	EU489100
Austrostipa pycnostachya (Benth.) S.W.L. Jacobs & J. Everett	Australia	*Peterson, Soreng & Rosenberg 14318* (US)	EU489394	EU489180	EU489247	EU489322	EU489101
Austrostipa scabra (Lindl.) S.W.L. Jacobs & J. Everett	Australia	*Peterson, Soreng & Rosenberg 14442* (US)	EU489395	EU489181	EU489248	EU489323	EU489102
Austrostipa scabra subsp. *falcata* (Hughes) S.W.L. Jacobs & J. Everett	Australia	*Blaylock 1496* (KW)	EU489396	EU489182	EU489249	EU489324	EU489103
Austrostipa tenuifolia (Steudel) S.W.L. Jacobs & J. Everett	Australia	*Peterson, Soreng & Macfarlane 14248* (US)	EU489397	EU489183	EU489250	EU489325	EU489104
Brachyelytrum erectum (Schreb.) P. Beauv.	USA	*Soreng 7440* (US)	EU489398	EU489184	EU489251	EU489326	EU489105

Taxon	Country	Voucher	trnK-matK	matK	trnH-psbA	trnL-trnF	ITS
Hesperostipa comata (Trin. & Rupr.) Barkworth ssp. *comata*	Canada	*Saarela, Sears & Maze 595* (UBC)	EU489399	EU489185	EU489252	EU489327	EU489106
Hesperostipa neomexicana (Thurb.) Barkworth	Mexico	*Peterson & Valdes-Reyna 18934* (US)	EU489400	EU489186	–	EU489328	EU489107
Hesperostipa spartea (Trin.) Barkworth	USA	*Holmes 214* (US)	EU489401	EU489187	EU489253	EU489329	EU489108
**Jarava atacamensis* (Parodi) Peñailillo[1]	Chile	*Peterson, Soreng, Finot & Judziewicz 15447* (US)	EU489402	EU489188	EU489254	EU489330	EU489109
**Jarava atacamensis* (Parodi) Peñailillo[2]	Chile	*Peterson, Soreng & Judziewicz 15480* (US)	EU489403	EU489189	–	EU489331	EU489110
**Jarava barrancaensis* (F.A. Roig) Peñailillo	Argentina	*Peterson & Annable 11371* (US)	EU489404	EU489190	EU489255	EU489332	EU489111
Jarava castellanosii (F.A. Roig) Peñailillo	Argentina	*Peterson & Annable 10336* (US)	EU489405	EU489191	EU489256	EU489333	EU489112
**Jarava chrysophylla* (E. Desv.) Peñailillo[1]	Argentina	*Peterson & Annable 11466* (US)	EU489406	EU489192	EU489257	EU489334	EU489113
**Jarava chrysophylla* (E. Desv.) Peñailillo[2]	Argentina	*Peterson, Soreng, Salariato & Panizza 19220* (US)	EU489407	EU489193	EU489258	EU489335	EU489114
**Jarava chrysophylla* (E. Desv.) Peñailillo[3]	Argentina	*Peterson, Soreng, Salariato & Panizza 19297* (US)	EU489408	EU489194	EU489259	EU489336	EU489115
**Jarava frigida* (Phil.) F. Rojas[1]	Argentina	*Peterson, Soreng, Salariato & Panizza 19360* (US)	EU489409	EU489195	EU489260	EU489337	EU489116
**Jarava frigida* (Phil.) F. Rojas[2]	Argentina	*Peterson & Annable 10397* (US)	–	EU489196	EU489261	EU489338	EU489117
**Jarava hieronymusii* (Pilg.) Peñailillo	Argentina	*Peterson & Annable 11488* (US)	EU489410	EU489197	EU489262	EU489339	EU489118
**Jarava humilis* (Cav.) Peñailillo[1]	Argentina	*Peterson & Annable 11258* (US)	EU489411	EU489198	EU489263	EU489340	EU489119
**Jarava humilis* (Cav.) Peñailillo[2]	Argentina	*Peterson & Annable 11317* (US)	EU489412	EU489199	EU489264	EU489341	EU489120
**Jarava humilis* (Cav.) Peñailillo[3]	Argentina	*Peterson, Soreng, Salariato & Panizza 19169* (US)	EU489413	EU489200	EU489265	EU489342	EU489121
Jarava hystricina (Speg.) Peñailillo	Argentina	*Peterson, Soreng, Salariato & Panizza 19550* (US)	–	–	–	–	EU489122
**Jarava ibarii* (Phil.) Peñailillo	Chile	*Soreng 7331* (US)	EU489414	EU489201	EU489266	EU489343	EU489123
Jarava ichu Ruiz & Pav.[1]	Peru	*Peterson, Soreng & Romaschenko 20745* (US)	EU489415	EU489202	EU489267	EU489344	EU489124
Jarava ichu Ruiz & Pav.[2]	Peru	*Peterson, Soreng & Romaschenko 20270* (US)	EU489416	EU489203	EU489268	EU489345	EU489125
Jarava juncoides (Speg.) Peñailillo	Argentina	*Ruiz Leal & Paci 465* (US)	EU489417	–	EU489269°	–	EU489126°
Jarava leptostachya (Griseb.) F. Rojas[1]	Argentina	*Peterson & Annable 11714* (US)	EU489418	EU489204	EU489270	EU489346	EU489127
Stipa leptostachya var. *capilliseta* (Hitchc.) Parodi[2]	Bolivia	*Villavicencio & Sukopp 52* (US)	–	–	EU489271	–	EU489128
Jarava media (Speg.) Peñailillo	Argentina	*Peterson, Soreng, Salariato & Panizza 19337* (US)	EU489419	EU489205	EU489272	EU489347	EU489129
**Jarava nicorae* (F.A. Roig) Peñailillo	Argentina	*Peterson & Annable 11408* (US)	EU489420	EU489206	EU489273	EU489348	EU489130
**Jarava patagonica* (Speg.) Peñailillo	Argentina	*Senn 4292* (US)	–	–	–	–	EU489131

Taxon	Country	Voucher	trnK-matK	matK	trnH-psbA	trnL-trnF	ITS
Jarava plumosa (Spreng.) S.W.L. Jacobs & J. Everett	Argentina	*Schinini, Vanni, Arbo, Horni & Aranda 29135* (US)	EU489421	–	EU489274º	EU489349	EU489132
Jarava plumosula (Nees ex Steud.) F. Rojas	Peru	*Peterson, Soreng & Romaschenko 20471* (US)	EU489422	EU489207	EU489275	EU489350	EU489133º
Jarava polyclada (Hack.) Peñailillo	Argentina	*Peterson & Annable 11569* (US)	EU489423	EU489208	EU489276	EU489351	EU489134º
Jarava pseudoichu (Caro) F. Rojas	Peru	*Peterson, Soreng & Romaschenko 20736* (US)	EU489424	EU489209	EU489277	EU489352	EU489135
Jarava scabrifolia (Torres) Peñailillo	Argentina	*Peterson & Annable 11712* (US)	EU489425	EU489210	EU489278	EU489353	EU489136
**Jarava speciosa* (Trin. & Rupr.) Peñailillo	Argentina	*Peterson & Annable 11549* (US)	EU489426	EU489211	EU489279	EU489354	EU489137
**Jarava speciosa* var. *major* (Speg.) Peñailillo[1]	Chile	*Soreng 7222* (US)	EU489427	EU489212	EU489280	EU489355	EU489138
**Jarava speciosa* var. *major* (Speg.) Peñailillo[2]	Argentina	*Peterson & Annable 11292* (US)	EU489428	EU489213	EU489281	EU489356	EU489139
**Jarava speciosa* var. *major* (Speg.) Peñailillo[3]	Argentina	*Peterson, Soreng, Salariato & Panizza 19216* (US)	EU489429	EU489214	EU489282	EU489357	EU489140
**Jarava vaginata* (Phil.) F. Rojas[1]	Argentina	*Peterson, Soreng, Salariato & Panizza 19222* (US)	EU489430	EU489215	EU489283	EU489358	EU489141
**Jarava vaginata* (Phil.) F. Rojas[2]	Argentina	*Peterson & Annable 11744* (US)	EU489431	EU489216	EU489284	EU489359	EU489142
Nardus stricta L.	Kyrgyzstan	*Soreng 7497* (US)	EU489432	EU489217	EU489285	EU489360	EU489143
Nassella brachychaetoides (Speg.) Barkworth	Bolivia	*Peterson & Annable 11748* (US)	EU489433	EU489218	EU489286	EU489361	EU489144
Nassella brachyphylla (Hitchc.) Barkworth	Bolivia	*Peterson, Soreng & Romaschenko 20631* (US)	EU489434	EU489219	EU489287	EU489362	EU489145
Nassella caespitosa Griseb.	Argentina	*Peterson, Soreng, Salariato & Panizza 19540* (US)	EU489435	EU489220	EU489288	EU489363	EU489146
Nassella clarazii (Ball) Barkworth	Argentina	*Peterson & Annable 11651* (US)	EU489436	EU489221	EU489289	EU489364	EU489147
Nassella dasycarpa (Hitchc.) Torres	Argentina	*Peterson & Annable 10344* (US)	EU489437	EU489222	EU489290	EU489365	EU489148
Nassella depauperata (Pilg.) Barkworth	Peru	*Cano et al. 13740* (USM)	EU489438	EU489223	EU489291	EU489366	EU489149
Nassella filiculmis (Delile) Barkworth	Chile	*Soreng 7009* (US)	EU489439	EU489224	EU489292	EU489367	EU489150
Nassella inconspicua (J. Presl) Barkworth	Bolivia	*Renvoize 5333* (US)	EU489440	–	EU489293	EU489368	EU489151
Nassella manicata (E. Desv.) Barkworth	Chile	*Soreng 7000* (US)	EU489441	EU489225	EU489294	–	EU489152º
Nassella meyeniana (Trin. & Rupr.) Parodi	Argentina	*Peterson & Annable 10301* (US)	EU489442	EU489226	EU489295	EU489369	EU489153º
Nassella nardoides (Phil.) Barkworth	Argentina	*Peterson & Annable 11773* (US)	EU489443	EU489227	EU489296	EU489370	EU489154º
Nassella neesiana (Trin. & Rupr.) Barkworth	Argentina	*Peterson & Annable 10258* (US)	EU489444	EU489228	EU489297	EU489371	EU489155
Nassella nidulans (Mez) Barkworth	Argentina	*Seijo 1871* (US)	EU489445	–	EU489298	–	EU489156º

Taxon	Country	Voucher	trnK-matK	matK	trnH-psbA	trnL-trnF	ITS
Nassella pfisteri (Matthei) Barkworth	Chile	*Soreng 7017a* (US)	EU489446	EU489229	EU489299	EU489372	EU489157
Nassella pubiflora (Trin. & Rupr.) E. Desv.	Argentina	*Peterson & Annable 11618* (US)	EU489447	EU489230	EU489300	EU489373	EU489158
Nassella rosengurttii (Chase) Barkworth	Uruguay	*Rosengurtt 216* (US-Type)	EU489448	–	EU489301	–	EU489159
Nassella rupestris (Phil.) Torres	Argentina	*Peterson & Annable 10347* (US)	EU489449	–	EU489302	EU489374	EU489160
Nassella sanluisensis (Speg.) Barkworth	Argentina	*Roig 3293* (US)	–	–	EU489303	EU489375	EU489161
Nassella sellowiana (Nees ex Trin. & Rupr.) Peñailillo	Brazil	*Reitz & Klein* 5314 (US)	–	–	EU489304	–	EU489162
Nassella tenuissima (Trin.) Barkworth	Argentina	*Pyke 992* (BC)	EU489450	EU489231	–	–	EU489163
Nassella trichotoma (Nees) Hack. ex Arechav.	Argentina	*Peterson & Annable 11506* (US)	EU489451	EU489232	EU489305	EU489376	EU489164
Piptochaetium brachyspermum (Speg.) Parodi	Argentina	*Peterson & Annable 11252* (US)	EU489452	EU489233	EU489306	EU489377	EU489165
Piptochaetium panicoides (Lam.) E. Desv.	Chile	*Soreng 7011* (US)	EU489453	EU489234	EU489307	EU489378	EU489166
Piptochaetium ruprechtianum E. Desv.	Argentina	*Peterson & Annable 11401* (US)	EU489454	EU489235	EU489308	EU489379	EU489167
Ptilagrostis mongholica (Turcz. ex Trin.) Griseb.	Kazakhstan	*Goloskokov s.n.* (LE)	EU489455	–	EU489309	EU489380	EU489168
Ptilagrostis porteri (Rydb.) W.A. Weber	USA	*Cooper* 1940 (US)	EU489456	EU489236	EU489310	EU489381	EU489169

American genera (*Aciachne*, *Lorenzochloa* Reeder & C. Reeder, *Ortachne* Nees ex Steud.), the North American genus *Oryzopsis* s.s., and North American species placed in *Piptatherum* (all other species are Old World), are not included in the present analysis because our preliminary data indicate that they have no effect on the disposition of taxa of concern here. One Asian species of *Ptilagrostis* Griseb. and five Australian species of *Austrostipa* S.W.L. Jacobs & J. Everett were included to show evidence of the geographical heterogeneity among some phylogenetic branches. Subsequent papers will include a much larger sample among the Stipeae. *Brachyelytrum erectum* and *Nardus stricta* were chosen as outgroups based on the results of recent analyses of phylogenetic relationships in *Pooideae* (Hilu et al. 1999; Soreng & Davis 2000; GPWG 2001; Davis & Soreng 2007; Soreng et al. 2007). These outgroups were used to root trees in the ITS analyses of the Stipeae (Jacobs et al. 2000; Romaschenko et al. 2007).

DNA extraction, amplification, and sequencing.—Leaf tissue was homogenized using Qiagen TissueLyser, and DNA was isolated using a BioSprint 96 DNA Plant Kit (Qiagen, Valencia, California, USA, 2005). For some specimens, the CTAB method (Doyle & Doyle 1987) was used.

PCR amplifications were performed in MJ Research or PE 9700 thermal cyclers. Genomic DNA was combined with 1x reaction buffer (200 mM Tris-HCl, 500 mM NH_4) (Bioline Biolase Taunton, Madison, USA) without Mg++, 2 mM $MgCl_2$, 200 mM dNTP's, 1.5µl of Taq polymerase (Bioline Biolase Taunton, Madison, USA), 40 pmol/µl each of forward and reverse primers.

The entire nuclear ribosomal ITS region was amplified using primers ITS1, ITS2, ITS3, ITS4, ITS5 (White et al. 1990) and ITS5A (Stanford et al. 2000) with the following thermal cycler settings: initial denaturation step of 2 min at 94°C, followed 35 cycles at 94°C for 30 s, 50–55°C for 30 s, 72°C for 1 min 30 s, and a final extension of 10 min at 72°C.

Four chloroplast DNA regions were sequenced: *trn*K-*mat*K, *mat*K, *trn*H^{GUG}-*psb*A, and *trn*L5'-*trn*F. The 5'-end of *trn*K-*mat*K and 5'- *mat*K were amplified separately. The 5'*trn*K-*mat*K readily amplified using the forward primer *trn*K3914F (Johnson & Soltis 1995) and newly designed reverse primer *trn*K660SR (5'-CGAATGATGATACATAGTGC-3') positioned close to the end of the 5'-*trn*K-*mat*K intron. The reverse complement (i.e. forward version) of the latter primer (*trn*K660SF; 5'-GCACTATGTATCATCATTCG-3') and the reverse complement of a slightly modified *mat*K1412F primer (Johnson & Soltis 1995; i.e., *mat*K1412SR 5'- CTGATACATAAGAGTTRTAT-3') were used to amplify ~555 pb of the 5'-end of *mat*K. The *trn*H^{GUG}-*psb*A intergenic spacer was amplified with primers *trn*H^{GUG} (Tate & Simpson 2003) and *psb*A (Sang et al. 1997). The *trn*L-*trn*F region (which included a portion of 3'-*trn*L intron, the 3'-*trn*L exon, and the *trn*L-*trn*F intergenic spacer) was amplified using primers 5'*trn*L^{UAA}(f) and *trn*F^{GAA}(c) [Taberlet et al. 1991]. The amplification parameters for all chloroplast regions were: 94°C, 2 min; 35 cycles of 94°C for 45 s, 58–62°C for 45 s, 72°C for 1 min 30 s; 72°C for 10 min. PCR products were cleaned with ExoSAP-IT (USB, Cleveland, Ohio, USA). DNA sequencing was performed with BigDye Terminator Cycle Sequencing v.3.1 (PE Applied Biosystems, Foster City, CA, USA) according to the following parameters: 80°C, 5 min; 25 or 30 cycles of 95°C for 10 s, 50°C for 5 s and 60°C for 4 min. Sequenced products were analyzed on an ABI PRISM 3730 DNA Analyzer 7900HT (ABI).

Sequences were aligned manually using BioEdit v.7.0.5.3 (Hall 1999) and then by eye. All sequences were submitted to GenBank (http://www.ncbi.nlm.nih.gov); voucher information, and GenBank accession numbers are provided in Table 1. Even though some indels, especially in chloroplast regions, seemed to be very specific for phylogenetic groups, they were not re-coded for this analysis and were excluded along with ambiguously aligned regions. The following gene regions were excluded: *trn*K-*mat*K with four regions of 2–25 bp in length; *trn*H-*psb*A with 10 regions of 1–4 (–22) bp in length; *trn*L-*trn*F with 31 regions from 1–6 (–20) bp; and ITS with 15 regions 1–4 (–22) bp. No regions were excluded from *mat*K. All gaps were treated as missing data. Parsimony analysis was performed using PAUP v. 4.0b10 (Swofford 2000) and PAUPRat v.1b (Sikes & Lewis 2001), which implements the Parsimony Ratchet of Nixon (1999). Parsimony searches were carried out for individual regions, combined plastid, and combined plastid and nuclear regions. In searching for the optimal tree, the heuristic method was implemented and tree bisection-reconnection (TBR)

was chosen as a branch swapping algorithm. Character states were specified as unordered and unweighted. PAUPRat searches were set for generating 1001 most parsimonious trees. Because PAUPRat finds the most parsimonious tree in each iteration, a set of 1001 iterations is recommended by program developers as sufficient to derive a consensus tree. All of the most parsimonious trees in our analyses were of the same length. These data sets were used to yield the majority-rule consensus trees.

Bayesian posterior probabilities were estimated using MrBayes v.3.01 (Huelsenbeck & Ronquist 2001; Ronquist et al. 2005) and the best-available substitution model was selected using MrModeltest 1.1b (Nylander 2002). The symmetrical model (SYM+I+G; Zharkikh 1994) with gamma-distributed rate variation across sites was selected by hierarchical likelihood ratio tests (hLRT) and Akaike information criterion. Bayesian analysis was initiated with random starting trees and was initially run for 1×10^6 generations with sampling frequency of the chains set to every 100^{th} iteration. If this number of generations was not sufficient for the Markov chains to reach stasis, additional generations were invoked. The standard deviation value of the split frequencies below 0.01 indicates that Markov chains reached their stasis (Ronquist et al. 2005). The number of generations needed to complete the analysis varied from 1×10^6 for individual DNA regions to 4×10^6 in analysis of the combined data. Branches with posterior probabilities (PP) >0.95 were considered statistically significant. For additional information about the stability of phylogenetic groups the branch frequency or parsimony frequency (BF) value was used. The BF value indicates how often a branch appeared in the analysis, i.e., when this value was 100% it means the node appeared unchanged in all iterations (i.e., strict consensus).

Bootstrap has a long history of being used as a standard measure when estimating phylogeny and we have included bootstrap analysis. Felsenstein (1985) states, "Bootstrapping provides us with a confidence interval within which is contained not the true phylogeny, but the phylogeny that would be estimated on repeated sampling of many characters from the underlying pool of characters." We agree with Felsenstein that bootstrap values are measures of repeatability rather than measures of accuracy (see Soltis & Soltis 2003). Regardless of interpretation, bootstrap values are affected by the number of characters supporting the clade of interest and the data set as a whole (Soltis & Soltis 2003). For a dataset with no conflict among characters, at least three characters are needed to provide 95% support (Felsenstein 1985). With real data a greater number of characters may be needed to achieve 95% support (Soltis & Soltis 2003). Thus bootstrap tends to be overly conservative, often underestimating a well-supported clade (Sanderson & Wojciechowski 2000). Bootstrap (BS) values were calculated using PAUP v. 4.0b10 (Swofford 2000) from 10×10^6 fast-heuristic bootstrap replicates with random addition sequence. Sequence divergence was calculated based on the uncorrected "p" distance measure included in Neighbor-joining search settings.

Scanning electron microscopy.—Lemma ultra structure was studied using dry mature seeds sampled from herbarium of the following species used in the phylogenetic analysis: *Jarava chrysophylla*, *Jarava speciosa*, *Jarava nicorae*, *Jarava pseudoichu*, *Jarava plumosula*, and *Amelichloa caudata*. Wax from the seed surface was removed by soaking the seeds in xylol solution for six to eight hours. After soaking, seeds were mounted on scanning electron microscopy sample tables. Mounted samples were covered with gold in the vacuum spray gun (JII-4X, Japan). The ultra structure of the lemma was studied using scanning electron microscope Jeol (JSM35C, Japan) at varying magnifications.

Light microscopy.—Cross-sections of leaf blades were prepared with the use of a rotary microtome. Intact leaf blades of *Jarava barrancaensis*, *Jarava speciosa* var. *major*, and *Jarava chrysophylla* from herbarium specimens were rehydrated for 10–12 min in distilled water at 100 °C. For studies of the sclerenchyma tissue, the cross-sections were stained with safranin.

RESULTS

Amplification of the *trn*K intron was significantly improved when the 5'-end of the intron and the maturase K gene were amplified separately. This enabled us to optimize our protocol for routine amplification of all chloroplast regions, even when old herbarium material was used. With this approach, PCR reactions were

up to 60% more successful than when the traditional intron primers were used (i.e., *trn*K3914F-2R). Consequently, the *trn*K[1] intron had the highest rate of amplification (92.6%) compared to the non-coding regions *trn*H-*psb*A (91.4%) and *trn*L-*trn*F (89%), which are traditionally considered to be the most easily amplified regions of the chloroplast genome (e.g., Kress et al. 2005). The *mat*K gene had a lower rate of amplification (85.2%); lack of *mat*K sequence data for a subset of taxa probably affected branch support in the combined chloroplast analysis. For the most of the silica preserved samples or recently collected herbarium specimens the entire ITS region was easily amplified (100%). A few specimens that lack several chloroplast regions were not included in the chloroplast analysis but we did include them in the combined analysis based on ITS and partial plastid sequences. A small subset of samples with two or more missing chloroplast regions was included in the combined analysis (see Table 1 for details). The plastid data set is missing 11.4% and the combined analysis is missing 9%, mostly due to unsequenced plastid regions for some samples. There is no missing ITS data.

Analyses of DNA sequences.—The general characteristics of the DNA regions used to infer phylogeny in our data set are detailed in Table 2. The greatest number of potentially parsimony informative characters per region was provided by the nuclear DNA ITS region.

The topologies of the trees produced by parsimony and Bayesian analyses for each of the four plastid regions sequenced were not inconsistent with that produced by the combined plastid data. Since the separate plastid datasets had comparatively low numbers of parsimony informative characters and low levels of sequence divergence they were combined (Fig. 1). The phylogenetic signals of the intergenic spacer *trn*H–*psb*A and *trn*L–*trn*F region were stronger than other gene regions and were slightly better resolved, partly due to their higher level of sequence divergence (Table 2).

No conspicuous differences between topologies derived from the *trn*H–*psb*A and *trn*L–*trn*F regions were found in this analysis. The only region that had informative substitutions responsible for separation of the *Pappostipa* clade of *Jarava* s.l. was the *trn*L–*trn*F region (data not shown).

The ITS tree was more than two times longer than the plastid tree and had lower CI and RI values (Table 2). There was relatively minor topological incongruence among clades in the trees generated from the combined plastid DNA-ITS data set (Fig. 3) and the ITS data (Fig. 2).

The monophyly of the Stipeae is well supported (BF=100, PP=0.64–1.00, BS=96–100) in all three cladograms (Figs. 1–3). Several major clades were consistently resolved in all three analyses (Fig. 1–3). A clade including *Achnatherum*, *Amelichloa, Austrostipa*, *Jarava* s.l., and *Nassella* [AAAJN] was detected in all three analyses (Figs. 1–3). Within the AAAJN clade a primary deep split between the *Pappostipa* clade and the clade of *Austrostipa* plus *Achnatherum*, *Jarava* (excluding the *Pappostipa* clade), *Nassella* and *Amelichloa* was maintained in all three analyses (Figs. 1–3). *Austrostipa* (from Australia) was resolved in all three analyses as sister to a clade of *Achnatherum*, *Jarava* (excluding the *Pappostipa* clade), *Nassella,* and *Amelichloa*; this relationship received strong support only in the nuclear and combined analyses. The latter clade is denoted in Figs. 1–3 as the Major American Clade or **MAC**.

Within MAC, *Achantherum* was always monophyletic and the sister group of the rest of the clade. A clade of *Nassella* with *Amelichloa* nested within it was detected in all three analyses (Figs. 1–3); this clade and always excluded elements of *Jarava*.

Table 2 summary statistics show the highest rate of parsimony informative characters, ingroup–outgroup and ingroup sequence divergence for nuclear rDNA ITS region. Analysis of the combined plastid-ITS data set (Fig. 3) showed deep splits among the American stipoids, also detected by the separate analyses, and separation of the *Pappostipa* clade. The Stipeae genera included in this analysis were resolved as monophyletic groups with three exceptions. *Ptilagrostis* resolved in a polytomy in the plastid analysis, but the species were united in the ITS and combined analyses. *Jarava* s.l. was divided into a *Pappostipa* clade and a *Jarava* s.s. (*Jarava* excluding the *Pappostipa* clade) clade (Fig. 3), or grade (Figs. 1&2). *Jarava* s.s. was resolved as a paraphyletic grade to *Nassella* (encompassing *Amelichloa*) in the independent plastid and ITS analyses, but the species were united in the combined analysis. Additionally, as detected in the separate plastid and ITS

TABLE 2. Summary of *trnK-mat*K, *mat*K, *trn*H-*psb*A, *trn*L-*trn*F, and ITS regions used in this study.

	***trn*K-*mat*K**	***mat*K**	***trn*H-*psb*A**	***trn*L-*trn*F**	**Combined plastid data**	**ITS**	**Combined plastid & nuclear data**
Sequence bp length (range)	571–556	555	585–567	612–541	2315–2231	592–584	2904–2271
Number of taxa	75	69	74	72	75	81	81
Number of characters	588	555	663	686	2537	640	3177
Number of informative characters	24	22	23	33	97	137	222
Ingroup-outgroup divergence (%)	3.62	4.22	5.2	7.35	–	14.34	–
Ingroup divergence (%)	0.79	0.78	0.87	0.84	–	4.31	–
Tree length	33	31	37	56	155	380	519
Consistency index (CI)	0.85	0.77	0.73	0.68	0.72	0.50	0.55
Retention index (RI)	0.98	0.95	0.96	0.93	0.95	0.82	0.87
Homoplasy index (HI)	0.15	0.22	0.27	0.32	0.27	0.50	0.44
Rescaled consistency index (RC)	0.83	0.74	0.70	0.63	0.68	0.40	0.48

analyses, *Nassella* was only resolved as monophyletic if *Amelichloa* is subsumed within it. Goodness-of-fit statistics i.e., consistency index, retention index, and rescaled consistency index, for the combined plastid DNA-nrDNA set was higher than for nrDNA set alone.

Early diverging clades at the base of the Stipeae included the genera *Ptilagrostis* (only as a polytomy in Fig. 1), *Anatherostipa*, and *Piptochaetium*. All analyses supported these genera as independent lineages at the current level of taxon sampling (Figs. 1–3). Resolution of relationships among these three genera varied among the datasets. Analysis of the plastid data set yielded a consensus topology with these genera and *Hesperostipa* in a polytomy with a large clade including *Jarava* s.l., *Austrostipa*, *Achnatherum*, *Nassella*, and *Amelichloa* [**AAAJN**]. Analysis of the ITS data set yielded a stepwise grade leading to *Hesperostipa* as sister group to AAAJN. The analysis of the combined plastid-nuclear data set resulted in a fully resolved and a moderately well supported resolved basal clade of *Ptilagrostis* as sister group to *Anatherostipa* and *Piptochaetium* (Fig. 3; BF=71, PP=0.93), and *Hesperostipa* as sister group to AAAJN (Fig. 3; BF=100, PP=1.00, BS=100). Henceforth, for ease of discussion, we call the set of *Anatherostipa*, *Piptochaetium* and *Ptilagrostis* the "***basal lineages***" (BL in Figs. 1–3). The position of these the basal lineages with respect to the core of the tree needs further examination, particularly including Old World genera, and is not the focus of the present study. Both of the *Piptochaetium* groups (Cialdella et al. 2007), *Piptochaetium* sect. *Podopogon* (Raf.) Parodi (*P. ruprechtianum*) and *Piptochaetium* sect. *Piptochaetium* (*P. panicoides*) are represented in the analysis. In all topologies, the *Piptochaetium* clade had high statistical support (BF=100, PP=0.95–1.00, BS=59–96; Figs. 1–3).

Representatives of the two extant geographical lineages of *Ptilagrostis* chosen for analysis were *P. mongholica* from Asia and *P. porteri* from the Americas. These species formed a consistent and well supported clade (BF=100, PP=1.00, BS=95) on the ITS tree (Fig. 2) and the combined tree (Fig. 3; BF=100, PP=1.00, BS=97). A phylogenetic relationship between these two species was resolved as a polytomy in the consensus tree from the plastid analysis (Fig. 1).

There are two clades adjacent to the basal lineages. One comprises the representatives of the genus *Hesperostipa* in a clade in all three trees (BF=100, PP=0.99–1.00, BS=99–100; Figs. 1–3). A second clade contains AAAJN members showing deep split (polyphyly) in the genus *Jarava*: *Stipa* subg. *Pappostipa* (*Pappostipa* clade) of Spegazzini (1901) elements of *Jarava* are separated from *Jarava* s.s. by sequentially diverging clades of *Austrostipa* and *Achnatherum* (BF=99–100; PP=0.63, <0.50, 0.99; BS=99, <50, 99; respectively in Figs. 1–3). In combined analyses as well as separate nuclear DNA ITS sequence analysis, the *Pappostipa* clade was well supported (BF=100, PP=0.95–1.00, BS=69–99; Figs. 2 & 3).

In all analyses, the Australian *Austrostipa* clade was sister group to MAC. These clades had high statistical support (BF=100; PP=0.68–1.00; BS=90, <50, 80; respectively in Figs. 1–3) and their relationship as sister clades was consistent.

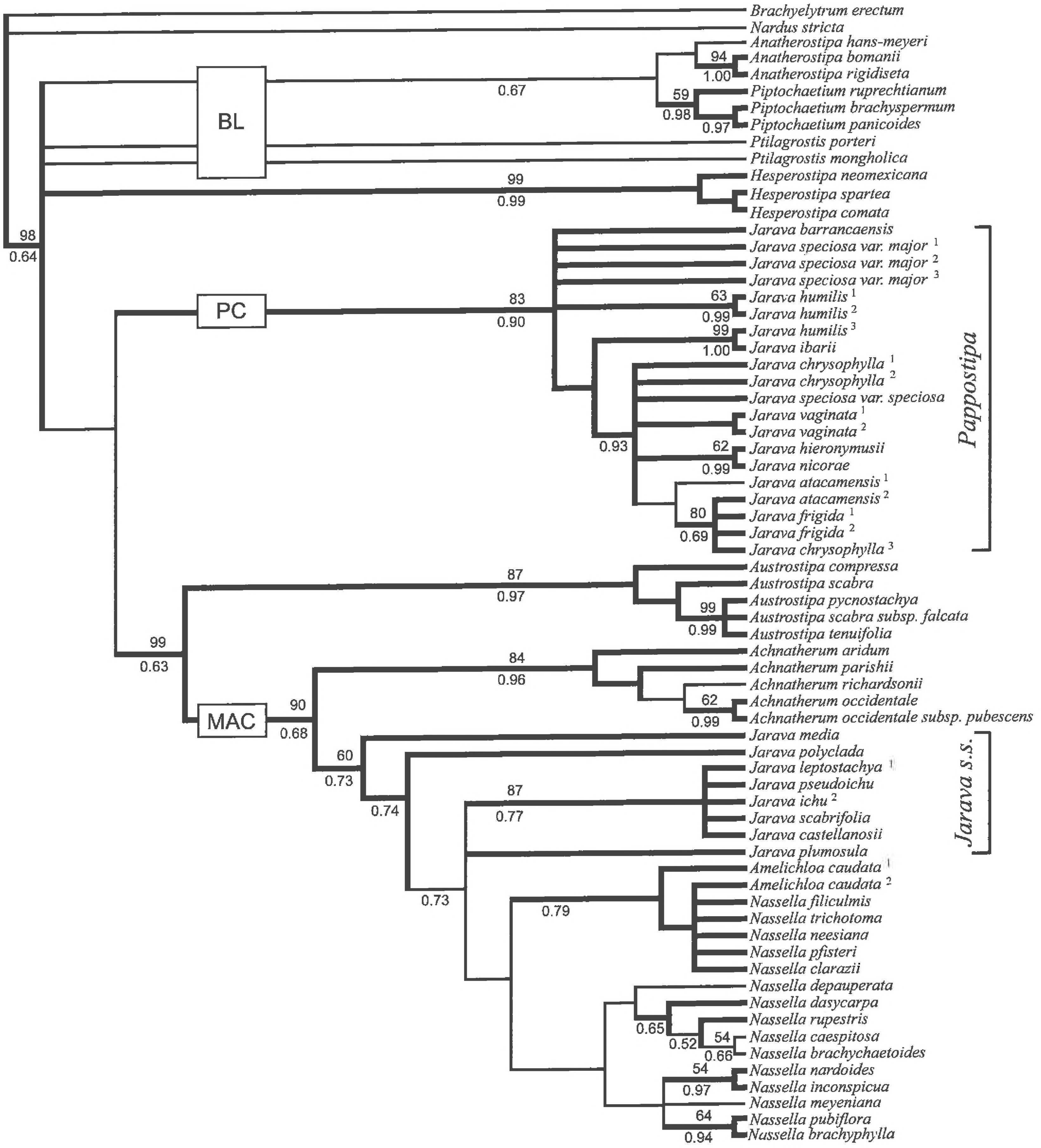


Fig. 1. Majority-rule consensus tree of 1001 most parsimonious trees based on maximum parsimony analysis of sequence data from chloroplast DNA *trn*K-*mat*K, *mat*K, *trn*H-*psb*A, and *trn*L-*trn*F regions. Branches in bold are present in the strict consensus tree, i.e. branch frequency (BF) equal to 100. Numbers above branches correspond to bootstrap (BS) values; numbers below branches correspond to Bayesian posterior probability (PP) values; BL=basal lineages; MAC=Major American Clade; PC=*Pappostipa* clade.

In the ITS and combined trees (Figs. 2 & 3) two major clades are resolved (with low support indices) within the *Pappostipa* clade: "P" that includes *Jarava barrancaensis*, *J. hieronymusii*, *J. nicorae*, *J. patagonica*, *J. speciosa* var. *major*, *J. speciosa* var. *speciosa*, and *J. vaginata* (BF=53, PP=<0.50–0.52); and "C" that includes *Jarava atacamensis*, *J. chrysophylla*, *J. frigida*, *J. humilis*, and *J. ibarii* (BF=97–100, PP=<0.50–0.90). Within all three trees (Figs. 1–3), *J. speciosa* var. *speciosa* and *J. speciosa* var. *major* never share a most-recent common

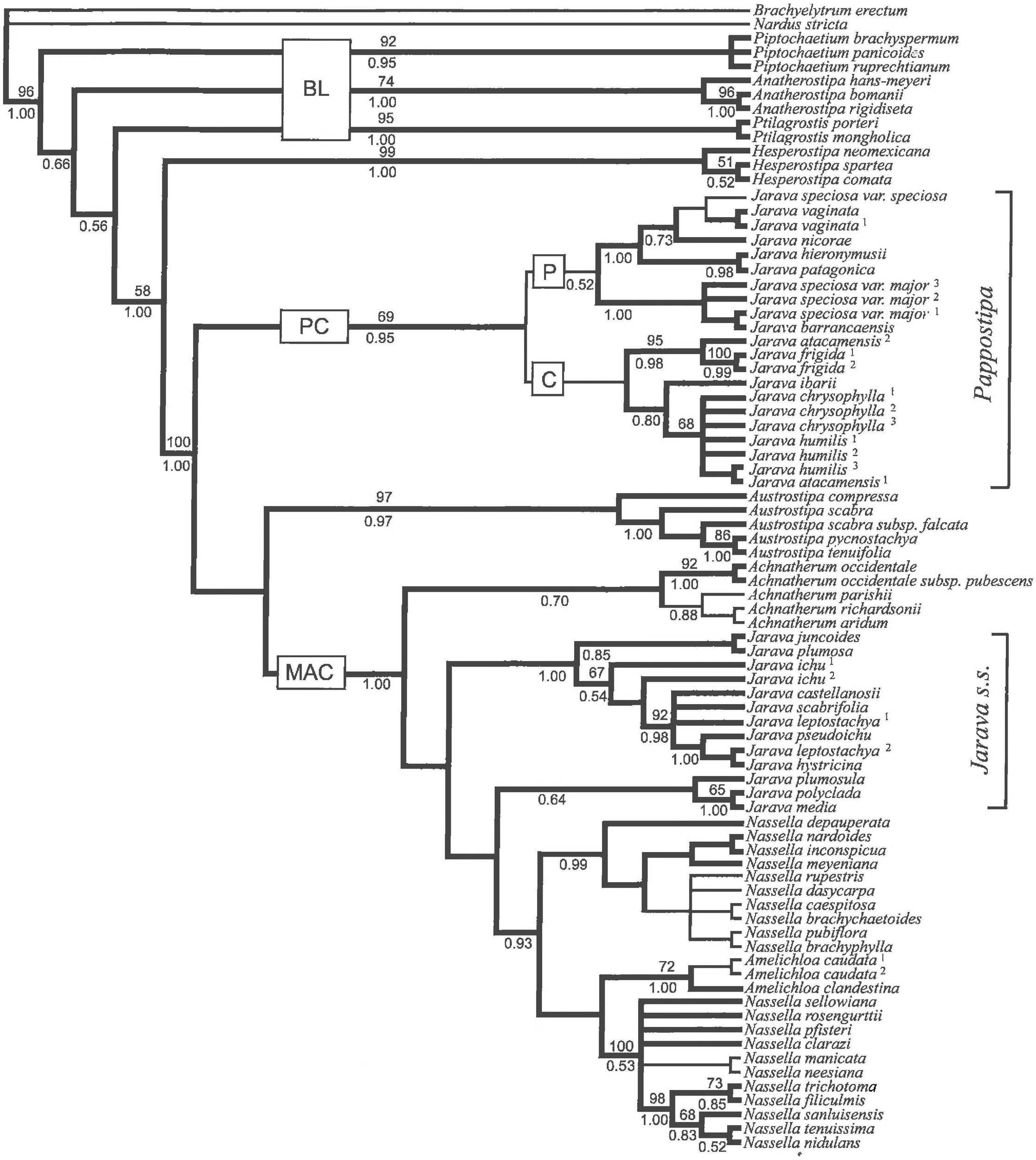


Fig. 2. Majority-rule consensus tree of 1001 equally most parsimonious trees based on maximum parsimony analysis of sequence data from nuclear rDNA ITS region. Branches in bold are present in the strict consensus tree, i.e., branch frequency (BF) equal to 100. Numbers above branches correspond to bootstrap (BS) values; numbers below branches correspond to Bayesian posterior probability (PP) values; BL=basal lineages; MAC=Major American Clade; PC=*Pappostipa* clade; C=*Pappostipa* sect. *Chrysovaginatae*; P=*Pappostipa* sect. *Pappostipa*.

ancestor. There is a distinct incongruence in the placement of *J. speciosa* var. *speciosa* in the plastid and nuclear trees (Figs. 1 & 2), but our plastid data currently provide little information on this discrepancy since there are only one or two apomophies found in the sequences of the *trn*L-F region.

In the three consensus trees (Figs. 1–3) MAC includes: a monophyletic *Achnatherum* (BF=100; PP=0.70–1.00; BS=84, <50, 76, respectively); a grade of four lineages (Fig. 1), two clades (Fig. 2), or a single clade (Fig. 3) for *Jarava*; and a single monophyletic clade of *Nassella* (including *Amelichloa*) (BF=61–100; PP

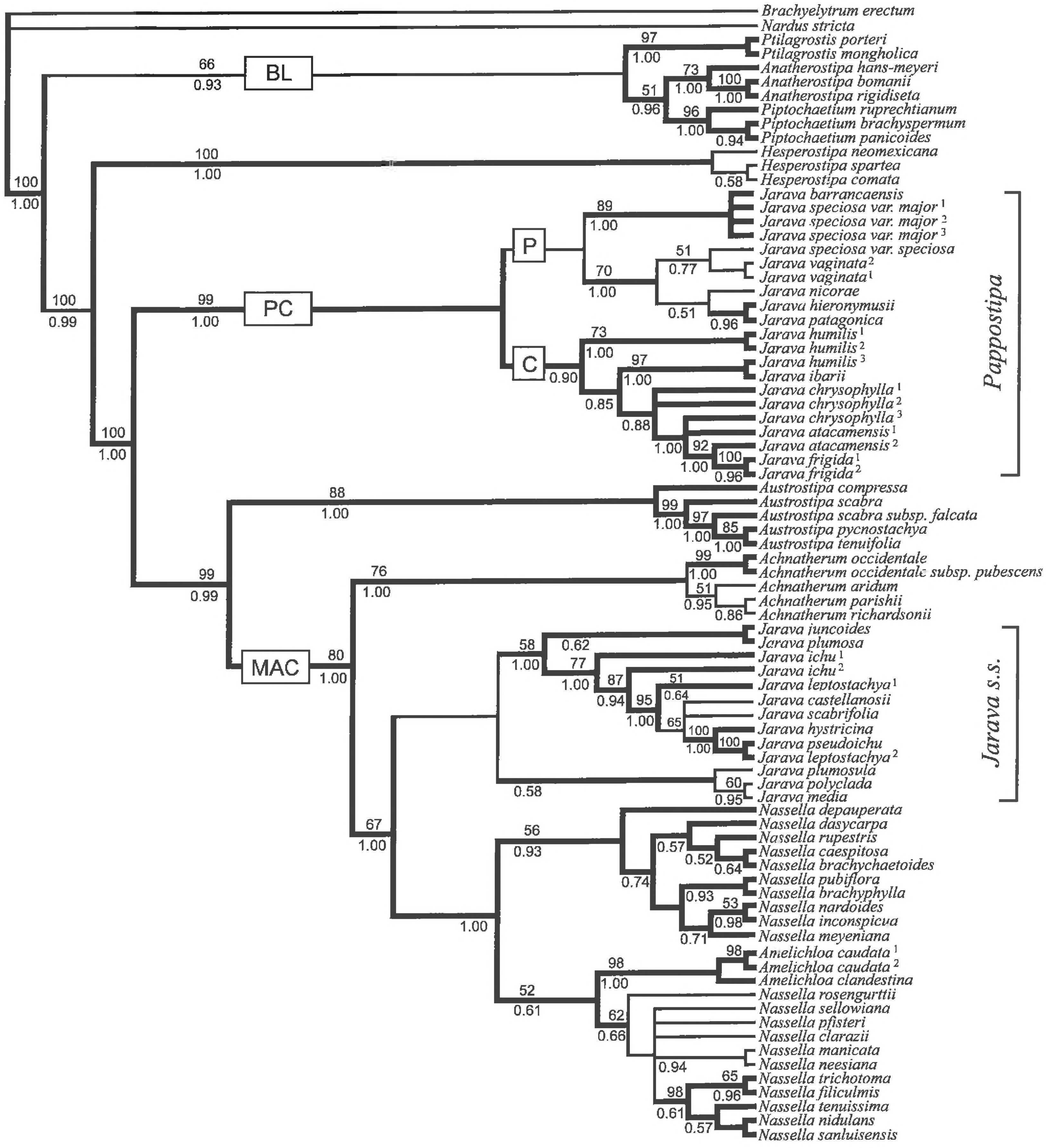


Fig. 3. Majority-rule consensus tree of 1001 equally most parsimonious trees based on maximum parsimony analysis of sequence data from chloroplast DNA *trn*K-*mat*K, *mat*K, *trn*H-*psb*A, and *trn*L-*trn*F regions and nuclear rDNA ITS region. Branches in bold are present in the strict consensus tree, i.e. branch frequency (BF) equal to 100. Numbers above branches correspond to bootstrap (BS) values; numbers below branches correspond to Bayesian posterior probability (PP) values; BL=basal lineages; MAC=Major American Clade; PC=*Pappostipa* clade; C=*Pappostipa* sect. *Chrysovaginatae*; P=*Pappostipa* sect. *Pappostipa*.

<0.50, 0.93, 1.00; Figs 2 & 3). *Jarava ichu*, the type species for the genus, resolved in a clade with *J. castellanosii, J. leptostachya, J. pseudoichu*, and *J. scabrifolia* in Fig. 1 (BF=100, PP=0.77, BS=87). Three *Jarava* species not in the plastid analysis, *J. hystercina, J. juncoides*, and *J. plumosa*, join the clade with the above set of species in Fig. 2 (BF=100, PP=1.00) and Fig. 3 (BF=100, PP=1.00, BS=58). In the combined analysis *Jarava media, J. plumulosa*, and *J. polyclada* are united as a sister clade to the above set (BF=100, PP= 0.58; Fig. 3). The latter three species formed a clade in the ITS analysis (BF=100, PP=0.64) that was sister group to *Nassella* includ-

ing *Amelichloa*, but were scattered elements of the grade of *Jarava* lineages leading to *Nassella* (including *Amelichloa*) represented in Fig. 1.

Our consensus trees indicate that *Nassella* is monophyletic (BF=61–100, PP=<0.50–1.00) only if *Amelichloa* is included. This conclusion is most strongly supported in the ITS and combined analyses (BF=100, PP 0.93–1.00). In our consensus trees there are two major clades within *Nassella*. One clade includes *N. brachychaetoides, N. brachyphylla, N. caespitosa, N. dasycarpa, N. depauperata, N. meyeniana, N. pubiflora, N. nardoises,* and *N. rupestris* (with *N. inconspicua* in Figs. 2 & 3; BF=100, PP= 0.93–0.99, BS=<50–56). The second clade includes *Amelichloa* species as sister group to the set of *N. clarazii, N. filiculmis, N. manicata, N. neesiana, N. nidulans, N. pfisteri, N. rosengurtii, N. sanluisensis, N. sellowiana, N. tenuissima,* and *N. trichotoma* (Figs. 2 & 3; BF=100, PP=0.53–0.66, BS=62–100), or *Amelichloa caudata*[1] as sister group to the set of *A. caudata*[2], *N. clarazii, N. filiculmis, N. neesiana, N. pfisteri, N. trichotoma*, and *A. clandestina* (Fig. 1; BF=100, PP=<0.50). *Amelichloa* is supported as monophyletic in the ITS and combined analyses (Figs. 2 & 3; BF=100, PP=100; BS=72–98).

Comparative morphology.—We evaluated a series of morphological and anatomical characters including: awn indumentum, form of the callus, lemma epidermis, and anatomy of the leaf blade in transverse section that differ among the hypothesized lineages of *Jarava* s.l. Nearly all samples of *Jarava* s.l. listed in Table 1 were surveyed and representative examples are given in Fig. 4. In addition, features of *Amelichloa* have also been evaluated.

Callus.—In the *Pappostipa* clade (Fig. 4A–C) the callus is acute to acuminate, sharp pointed; the angle between the callus base plane and floret axis is low; callus base is lanceolate; peripheral ring is marginiform, with proximal borders near one another, not fused nor thin, leaving an open foveola (literally, "small depression or scar"; the term used to name the section of conducting bundle at the base of the callus, but not only its open ventral part as it was for species resolved here in the *Pappostipa* clade by Roig 1964); distal, flat prow of the peripheral ring is not developed or is moderately developed. The foveola is fusiform or lanceolate, usually the same shape as the peripheral ring.

In the *Jarava ichu* group (Fig. 4D) the callus is short, truncate, blunt to acute; the angle between the callus base plane and floret axis is higher than in *Pappostipa* clade; callus base is obovate or ovate, rarely orbicular or lanceolate; peripheral ring is marginiform to flat, proximal borders not near each other, thinned and not fused, leaving the foveola open; distal, flat prow of the peripheral ring is not developed, inconspicuous or is slightly conspicuous. The foveola is obovate, ovate or orbicular, rarely lanceolate, and usually the same shape as the peripheral ring.

In *Jarava media, J. plumosula,* and *J. polyclada,* (Fig. 4E) the callus is acute, sharp pointed; the angle between the callus base plane and floret axis is high; callus base is ovate or acuminate, tapering to the relatively long but obtuse point; peripheral ring is flat or slightly marginiform, proximal borders joined, usually fused and not thinned, closing the foveola; distal, flat prow of the peripheral ring is well developed, characteristically fused at the base. The foveola is oval or orbicular and does not follow the shape of peripheral ring.

In *Amelichloa caudata* and *A. cladestina* (Fig. 4F) the callus is short, blunt; the angle between the callus base plane and floret axis is high; callus base is obovate or oblong; peripheral ring is conspicuously marginiform, proximal borders not near each other, thinned, leaving the foveola open; distal, flat prow of the peripheral ring is not developed or is inconspicuous. The foveola is oval or oblong ellipsoid and usually follows the shape of the peripheral ring.

Lemma epidermis.—In species of the *Pappostipa* clade (Fig. 4G) the epidermal fundamental cells regularly alternate with silica cells and are all approximately the same length or shorter than the silica cells; end walls are straight or slightly uneven, sidewalls slightly sinuate; silica bodies are oval to oblong rectangular, slightly unequal. In the *Jarava* s.s. group (Fig. 4H) the epidermal fundamental cells regularly alternate with silica cells and are considerably shorter than the silica cells (designated here as "maize" pattern); end walls are straight, sidewalls thin-walled, lacking silica, straight or slightly uneven; silica bodies are short rectangular, often equal. In *Amelichloa caudata* and *A. clandestina* (Fig. 4I) the epidermal fundamental cells are usually ir-

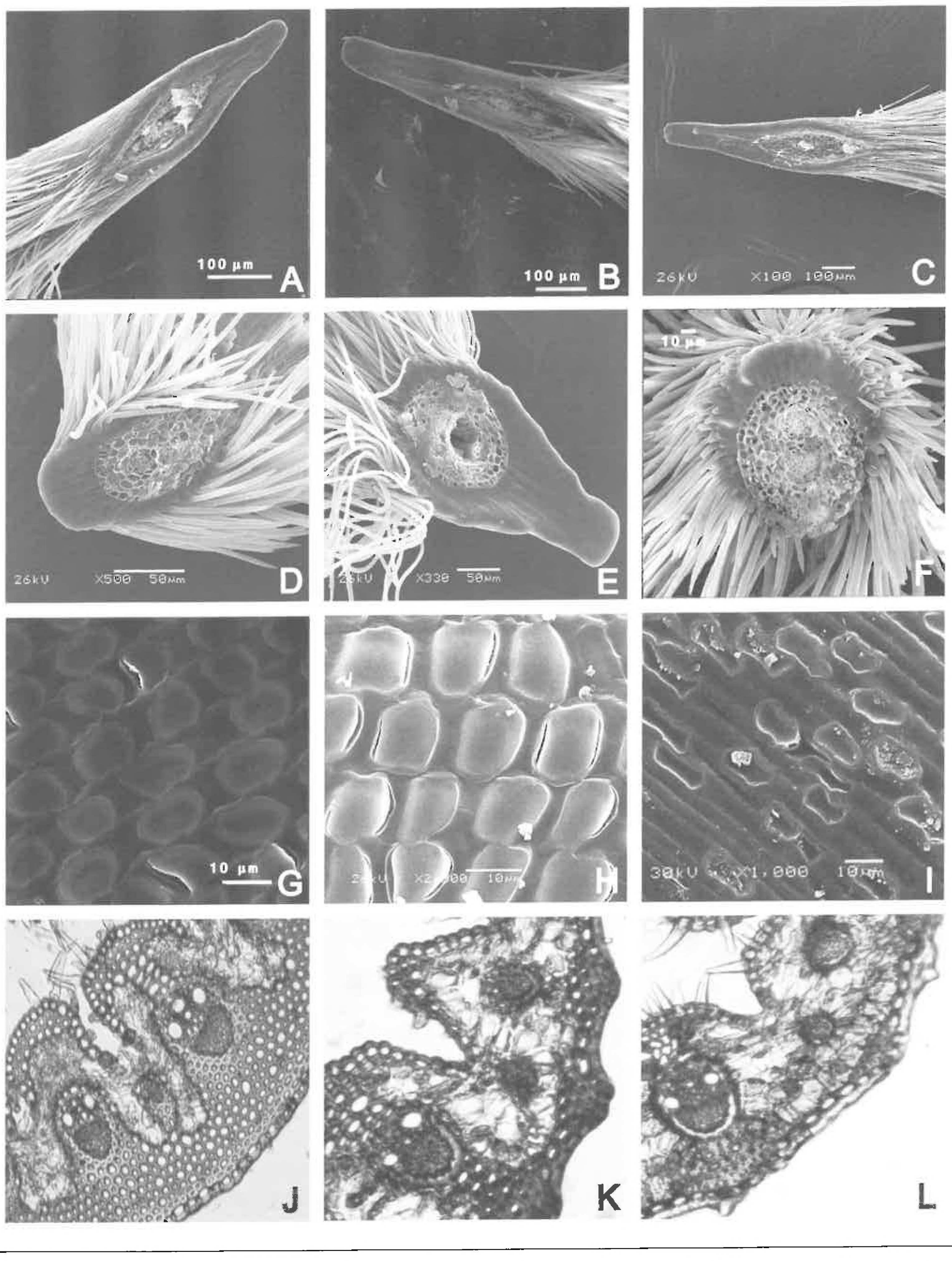


Fig. 4. Morphological and anatomical features of American Stipeae. **A.** Acute callus base of *Pappostipa chrysophylla* [*Peterson & Annable 11466* (US)]. **B.** Acute callus base of *Pappostipa speciosa* [*Peterson & Annable 11549* (US)]. **C.** Acute callus base of *Pappostipa nicorae* [*Peterson & Annable 11408* (US)]. **D.** Truncate callus base of *Jarava pseudoichu* [*Peterson, Soreng & Romaschenko 20471* (US)]. **E.** Acute callus base of *Jarava plumosula*.[*Peterson, Soreng & Romaschenko 20736* (US)]. **F.** Obovate callus base of *Amelichloa caudata* [*Peterson & Annable 11398* (US)]. **G.** Lemma epidermal fundamental cells are about the same size or shorter than the silica cells in *Pappostipa chrysophylla*. **H.** Lemma epidermal fundamental cells are larger than the silica cells in *Jarava pseudoichu*. **I.** Lemma epidermal fundamental cells are usually irregularly alternate with silica cells, and are shorter to approximately three times the length of the silica cells; endwalls are straight or slightly uneven, sidewalls sinuate in *Amelichloa caudata*. **J.** Basal leaf blade cross-section showing well developed adaxial ribs and furrows of *Pappostipa barrancaensis* [*Peterson & Annable 11371* (US)]. **K.** Basal leaf blade cross-section showing well developed adaxial ribs and furrows of *Pappostipa major* [*Soreng 7222* (US)]. **L.** Basal leaf blade cross-section showing inconspicuous ribs and furrows of *Pappostipa chrysophylla*.

regularly alternate with silica cells, and are shorter to approximately three times the length of the silica cells; end walls are straight or slightly uneven, sidewalls slightly sinuate; silica bodies are oblong, unequal.

Leaf blade transection.—Basal leaf blade cross-sections from *Jarava barrancaensis*, *J. speciosa* var. *major*, and *J. chrysophylla* are shown in Fig. 4J–L, and represent anatomical forms in the *Pappostipa* clade. We found two distinct types of leaf morphology and anatomy as detected by Arriaga (1983) that correspond with the two subclades **P** and **C** in our trees (Figs. 2&3). The P clade has type I leaf blade anatomy (incl. *Jarava barrancaensis*, *J. hieronymusii*, *J. nicorae*, *J. patagonica*, *J. speciosa* var. *major*, *J. speciosa* var. *speciosa*, and *J. vaginata*) with stiff, relatively thick usually pungent leaf apices, adaxial ribs well developed, separated by deep furrows; primary veins (vascular bundles) are numerous (5 or 6), often adaxially and abaxially connected by sclerenchyma girders (rarely by transitional parenchyma girders; Fig. 4J); tertiary veins are often abaxially connected by sclerenchyma girders; bulliform cells are present at the bottom of all furrows; abaxial sclerenchyma is continuous; adaxial sclerenchyma is discontinuous (Fig. 4K).

The C clade (Figs. 2&3) has type II leaf blade anatomy (incl. *Jarava atacamensis*, *J. frigida*, *J. humilis*, and *J. ibarii*) with slender, usually non-pungent leaf apices, adaxial ribs not well developed separated by shallow furrows; primary veins not numerous (1–3, rarely to 4), often only abaxially connected by sclerenchyma girders (rarely adaxially connected at the midrib); tertiary veins are often not connected by sclerenchyma; bulliform cells are present only close to the midrib; abaxial sclerenchyma is discontinuous; adaxial sclerenchyma is usually absent or residual (Matthei 1965; Arriaga 1983). *Jarava chrysophylla* (Fig. 4L) differs from the previous type by having clearly discontinuous abaxial sclerenchyma and tertiary veins that are adaxially connected by sclerenchyma girders in a compound midrib.

TAXONOMY

The phylogenetic information provided by our DNA analyses coupled with significant morphological differences among the *Jarava* s.l. clades detected, forces us to recognize the *Pappostipa* clade as an independently derived monophyletic genus if we are to maintain the monophyletic status of the other genera currently recognized in the AAAJN clade. Here we propose combinations in the new genus *Pappostipa* for all 14 species resolved in this clade in our DNA analyses, and *Stipa speciosa* f. *major* which is raised to the rank of species in *Pappostipa*. Eight additional species are transferred to *Pappostipa* that were formerly included in *Stipa* subg. *Pappostipa* by Parodi (1960) and or *Jarava* s.l. by Peñalillo (2002, 2003), based on their shared morphology with the DNA tested set of species. All currently accepted infraspecific taxa (Peñalillo 2003) in these 23 species are also transferred to *Pappostipa*. Leaf anatomy types described by Parodi (1960) and Arriaga (1983) correlated with the two *Pappostipa* subclades (P & C) detected in our DNA analysis. Further review of *Pappostipa* leaf blade and sheath morphology after our DNA analyses (based on Roig 1964, Nicora & Rúgolo de Agrasar 1978, and pers. obs.), continue to support this correlation. Therefore we conclude that *Pappostipa* can be divided into two morphologically distinct sections of 14 (*P.* sect. *Pappostipa*) and nine (*P.* sect. *Chrysovaginatae*) species.

Pappostipa (Speg.) Romaschenko, P.M. Peterson & Soreng, comb. et stat. nov. Basionym: *Stipa* subg. *Pappostipa* Speg., Anales Mus. Nac. Montevideo 4:III, 45. 1901. Synonym *Stipa* sect. *Papoforeas* E. Desv., Fl. Chil. 6:278. 1854. Type: *Stipa speciosa* Trin. & Rupr. (lectotype, designated here).

Plants perennial, caespitose, sometimes with stolons. Culms 10–70 cm long, erect or geniculate, with two or three nodes, often concealed by sheaths; basal branching intravaginal. Basal leaves (6–)10–40(–60) cm long, (0.5–)0.7–2.3(–2.5) wide, convolute, apices acuminate, sometimes pungent; adaxial surface pilose and sulcate, the furrows 8–13 or only 3–6; abaxial surface glabrous, scabrous, occasionally with macrohairs; sheaths glabrous or pubescent, open, whitish, pale or stramineous to brownish-red, reddish or purplish; ligules 0.5–1(–3) mm long, truncate, membranous, ciliate, or pilose. Flag leaves 4–15 cm long, sometimes deciduous; ligules 2–5 mm long, elongated. Panicles 30–240 mm long, with 5–50 spikelets, often compact, included or exserted in the upper leaf sheath; pedicels 0.5–12 mm long, often hairy. Glumes 15–45 mm long, subequal or slightly unequal, longer than floret, acuminate, hyaline, (1–)3–5-nerved, purplish, green-

ish, rarely plumbeous. Florets fusiform, terete. Calluses 1–4 mm long, often pilose, apex obtuse to truncate; foveolas proximally opened, often the shape of peripheral rings, fusiform or lanceolate; peripheral rings thickened near the margins, flat prow usually not developed. Lemmas 4–16(–17) mm long, chartaceous, entirely pubescent with short appressed hairs or dorsally glabrous along the upper ½ of the lemma, rarely hairs gradually elongate toward the base of the column or dorsally glabrous; prickles (hooks) usually present in the upper part; lobes up to 1 mm long; apices not fused into a crown. Awns 20–70(–193) mm long, persistent, once geniculate; columns 15–33 mm long, sometimes protruding above glumes, plumose, hairs 4–9 mm long; bristles 12–45(–170) mm long, equal to much longer than columns, scabrous, smooth or glabrous, sometimes pungent, pale to chestnut colored or black, straight, rarely sinuous or falcate. Paleas 4–13 mm long, usually subequal to lemmas, occasionally ½ as long as the lemmas or shorter, linear, linear-cuneate or elongate, hyaline, often dorsally hairy, exceptionally glabrous, two-nerved, rarely nerves extended as short awns, these not conspicuous. Lodicules 3. Stamens 3, anthers yellow or purplish.

Pappostipa sect. **Pappostipa,** sect. nov. Type: *Pappostipa speciosa* (Trin. & Rupr.) Romaschenko.

Pappostipa sect. *Pappostipa* differs from *P.* sect. *Chrysovaginatae* by having basal sheaths that are brownish-red, pink, or purplish and basal leaf blades that are stiff, relatively thick with pungent apices and usually with well developed adaxial ribs separated by deep furrows (referred to as type I leaf anatomy in Arriaga 1983).

"Short-bristle" group

The following species all share comparatively a short final segment of the awn (referred to as a bristle; Jacobs et al. 1995) that is 1.5–2 times shorter than the bristles in the "long-bristle" group, of *P.* sect. *Pappostipa*.

Pappostipa speciosa (Trin. & Rupr.) Romaschenko, comb. nov. Basionym: *Stipa speciosa* Trin. & Rupr., Sp. Gram. Stipac. 45. 1842. *Stipa humilis* var. *speciosa* (Trin. & Rupr.) Kuntze, Revis. Gen. Pl. 3(3):371. 1898. *Achnatherum speciosum* (Trin. & Rupr.) Barkworth, Phytologia 74:13. 1993. *Jarava speciosa* (Trin. & Rupr.) Peñailillo, Gayana, Bot. 59(1):32. 2002. Type: CHILE: *H. Cuming s.n.* (holotype: LE-TRIN–1443.01!; isotype: US-557434 fragm. ex LE!).

Pappostipa speciosa var. **manqueclensis** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *manqueclensis* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 12:89, t. 5. 1965. *Jarava speciosa var. manqueclensis* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: San Carlos, Pampa de Las Cortaderas, *F. Roig 5339* (holotype: MERL).

Pappostipa speciosa var. **atuelensis** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* f. *atuelensis* F.A. Roig. Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 12(1):91–94, lamina 6. 1–9. 1965. *Stipa speciosa* var. *atuelensis* (F.A. Roig) F.A. Roig, Deserta 2:113. 1971. *Jarava speciosa* var. *atuelensis* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Mendoza: Depto. San Rafael, Sosneado, en márgenes del Río Atuel, *A. Ruiz Leal 23229* (holotype: MERL).

Pappostipa speciosa var. **parva** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *parva* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):33–35. 1964 [1966]. *Jarava speciosa* var. *parva* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, 2800m,18–19 Jan 1938, *A. Ruiz Leal 4880* (holotype: MERL).

Pappostipa speciosa var. **breviglumis** (Parodi) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *breviglumis* Parodi, Revista Argent. Agron. 27(3–4):74, f. 1, B, b, i. 1960. *Jarava speciosa* var. *breviglumis* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. San Juan: Depto. Iglesia, al norte de Rodeo, Mina Fierro Nuevo, 24 Feb 1950, *V.R. Perrone 54904 1/2* (holotype: BAA).

Pappostipa speciosa var. **ciliata** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *ciliata* F.A. Roig, Giorn. Bot. Ital. 121(1–2):43, f. 2. 1987.*Jarava speciosa* var. *ciliata* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. San Juan: Iglesia, entre Tocota y Cuesta de los Heladeros, 5 Mar 1962, 2180m, *A. Ruiz Leal 22093* (holotype: MERL; isotype: SI).

Pappostipa speciosa f. **horrida** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* f. *horrida* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):36, t. 25a. 1964 [1966]. *Jarava speciosa* f. *horrida* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Malalhue, Cerro Huemul, frecuente, matas aisladas, rígidas, pinchudas, 14 Jan 1958, *A. Ruiz Leal & F.A. Roig 18784* (holotype: MERL?).

Pappostipa speciosa f. **abscondita** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* f. *abscondita* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):36–37. 1964 [1966]. *Jarava speciosa* f. *abscondita* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Uspallata, Cumbre del Paramillo, 11 Feb 1964, *F.A.. Roig 4929* (holotype: MERL).

Pappostipa speciosa var. **media** (Torres) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *media* Torres, Comis. Invest. Ci. [Buenos Aires] 12:44, t.1, C, c; t.4d. 1993. *Jarava speciosa* var. *media* (Torres) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Buenos Aires: Pdo. Villarino, Laguna Chasicó; 19 Apr 1976, *J. Frangi 79* (holotype: LP).

Pappostipa vaginata (Phil.) Romaschenko, comb. nov. Basionym: *Stipa vaginata* Phil., Linnaea 33(3–4):281. 1864. *Jarava vaginata* (Phil.) F. Rojas, Gayana, Bot. 54(2):173. 1997 [1998]. Type: CHILE. Aconcagua: S. Felipe, Nov 1862, *Landbeck s.n.* (holotype:?; isotypes: SGO-45662, US-81900 fragm. ex W!).

Pappostipa vaginata f. **rigida** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* f. *rigida* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):54–55. 1964 [1966]. *Jarava vaginata* f. *rigida* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, Cumbre del Paramillo, 2850m, 11 Feb 1964, *F.A. Roig 4927* (holotype: ?; isotype: LP).

Pappostipa vaginata f. **inmersa** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* f. *inmersa* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):53–54, t. 10 & 25e. 1964 [1966]. *Jarava vaginata* f. *inmersa* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Cumbre del Paramillo de Uspallata, 2800m, 22 Jan 1960, *F.A. Roig 4319* [*F.A. Roig 4308* cited also in parentheses with 4319] (holotype: MERL?; isotype: LP).

Pappostipa vaginata f. **laevis** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* f. *laevis* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2): 52, t. 10 & 25g. 1964 [1966]. *Jarava vaginata* f. *laevis* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, 2800m, 22 Jan 1960, *F.A. Roig & A. Ruiz Leal 4318* (holotype: MERL?).

Pappostipa vaginata f. **contracta** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* f. *contracta* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):53, t. 10 & 25f. 1964 [1966]. *Jarava vaginata* f. *contracta* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Los Hornillos, 10 Jan 1959, *A. Ruiz Leal 20144* (holotype: MERL herb. F.A. Roig 3405; isotype: LP).

Pappostipa vaginata var. **argyroidea** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* var. *argyroidea* F.A. Roig, Deserta 2:107, t. 1. 1971.*Jarava vaginata* var. *argyroidea* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Mendoza: Depto. Malalhue, entre Cañada Colorada y Fortín Malalhue, 9 Nov 1960, *F.A. Roig 4514* (holotype: MERL?; isotype: LP ex Herb. Roig 4514).

Pappostipa vaginata var. **dilatata** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* var. *dilatata* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):54. 1964 [1966]. *Jarava vaginata* var. *dilatata* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Camino a Uspallata por Potrerillos, ala vera del mismo, en suelos removidos, arenosos, 22 Dec 1961, *A. Ruiz Leal, Roig & Wainstein 4523* (holotype: ?; isotype: LP).

Pappostipa nicorae (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa nicorae* F.A. Roig, Giorn. Bot. Ital. 121(1–2):41, f. 1. 1987. *Jarava* nicorae (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):32. 2002. Type: ARGENTINA. San Juan: Depto. Iglesia, Reserva de San Guillermo, Cajoncito de la Brea al N del Infiernillo, 3680m, 20 Feb 1981, *E. Nicora, Guaglianone & Ragonese 8201* (holotype: SI; isotype: LP).

Pappostipa hieronymusii (Pilg.) Romaschenko, comb. nov. Basionym: *Stipa hieronymusii* Pilg., Bot. Jahrb. Syst. 56 (Beibl. 123):24. 1920. *Jarava hieronymusii* (Pilg.) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA. La Rioja: Depto. Gral. Sarmiento, Cuesta del Peñón al sur de la Laguna Brava, Cordillera de La Rioja, 26 Feb 1879, *G. Hieronymus & G. Niederlein 314* (holotype: B; isotypes: BAA-3071 fragm. ex B, CORD, US-866109 fragm!).

Pappostipa patagonica (Speg.) Romaschenko, comb. nov. Basionym: *Stipa patagonica* Speg., Revista Fac. Agron. Veterin. (Buenos Aires) 3:581. 1897. *Jarava patagonica* (Speg.) Peñailillo, Gayana, Bot. 59(1):32. 2002. Type: ARGENTINA. Santa Cruz: Río Santa Cruz, Feb 1882, *C. Spegazzini s.n.* (lectotype: LP ex LPS–2433 designated by L.R. Parodi, Revista Argent. Agron. 27(3–4):72. 1960; isolectotypes: BAA, LPS).

Pappostipa maeviae (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa maeviae* F.A. Roig, Bol. Soc. Argent. Bot. 14(4):314, f. 2. 1972. *Jarava maeviae* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA. Neuquén: Depto. Chos Malal, filo SE del volcán Domuyo, en pedregales, s. d., *O. Boelck 11290* (holotype: BAA; isotype: BAB).

Pappostipa parodiana (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa parodiana* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):44–46, t. 8, 26b. 1964 [1966]. *Jarava parodiana* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA: Malalhue, Ranquil de Lirkai, 1100m, frecuente en las laderas empinadas de los cerros, 14 Dec 1960, *A. Ruiz Leal 21453* (holotype: MERL).

Pappostipa braun-blanquetii (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa braun-blanquetii* F.A. Roig, Phytocoenologia 2(1–2):19, f. 1. 1975. *Jarava braun-blanquetii* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Mendoza: San Rafael, Valle de Las Leñas, 13 Jan 1970, A. Ruiz Leal 27150 (holotype: MERL; isotype: LP).

Pappostipa semperiana (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa semperiana* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):37t. 6, 25d. 1964 [1966]. *Jarava semperiana* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA: Las Heras, entre Uspallata y Puesto San Alberto (La Arboleda), 27 Dec 1947, *A. Ruiz Leal 11138* (holotype: MERL).

Pappostipa ruiz-lealii (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa ruiz-lealii* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):42, t. 5, 25c. 1964 [1966]. *Jarava ruiz-lealii* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, 2800m, 23 Jan 1960, *A. Ruiz Leal & F.A. Roig 20774* (holotype: MERL-20774).

"Long-bristle" group

The following four species all share the unique characteristic of having the final segment of the awn (referred to as a bristle; Jacobs et al. 1995) as being 1.5–2 times longer than the bristles in the "short-bristle" group of species of *P.* sect. *Pappostipa*.

Pappostipa malalhuensis (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa malalhuensis* F.A. Roig, Revista Fac. Ci.

Agrar. Univ. Nac. Cuyo 11(1–2):60–62, t, 13, 25d. 1964 [1966]. *Jarava malalhuensis* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: ARGENTINA: Malalhue, Potí Malal, n.v. "coirón blanco," 13 Jan 1960, *A. Ruiz Leal 20938* (HOLOTYPE: MERL-20938).

Pappostipa major (Speg.) Romaschenko, comb. et stat. nov. BASIONYM: *Stipa speciosa* f. *major* Speg., Anales Mus. Nac. Montevideo 4(2):58, f. 10a–b. 1901. *Stipa speciosa* var. *major* (Speg.) Parodi, Revista Argent. Agron. 27(3–4): 75, f. 1, C, c. 1960. *Jarava speciosa* var. *major* (Speg.) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA: vulgato prope Lago Nahuelhuapi, Jan 1900, *E. Fernádez s.n.* (SYNTYPE: ?). Neuquen: in Valle Trolope, Feb 1900, *Otto Asp s.n.* (SYNTYPE: ?).

Pappostipa major can be separated from *P. speciosa* by having longer glumes, narrower and convolute leaf blades, longer bristles usually 1.5 to 2 times as long, black (yellow in *P. speciosa*) bristles, larger anthecia, and a chromosome base number of $2n=60$ ($2n=66$ in *P. speciosa*) [Parodi 1960; Stebbins & Löve 1941; Covas & Bocklet 1945]. Futhermore, these varieties were resolved independently of one another in both the plastid and ITS DNA analyses (**Figs. 1, 2 & 3**).

Pappostipa vatroensis (F.A. Roig) Romaschenko, comb. nov. BASIONYM: *Stipa vatroensis* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):40–42, t. 7, 26a. 1964 [1966]. *Jarava vatroensis* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1): 31.2002. TYPE: ARGENTINA: Malalhue, el Vatro, 1100m, en la margen izquierda del río Barrancas, en laderas, 16 Dec 1960, *A. Ruiz Leal 21501* = *F.A. Roig 3765* (HOLOTYPE: MERL).

Pappostipa barrancaensis (F.A. Roig) Romaschenko, comb. nov. BASIONYM: *Stipa vatroensis* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):40–42, t. 7, 26a. 1964 [1966]. *Jarava barrancaensis* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: ARGENTINA: Malalhue, el Vatro, 1100m, en la margen izquierda del río Barrancas, en laderas, 16 Dec 1960, *A. Ruiz Leal 21501* = *F.A. Roig 3765* (HOLOTYPE: MERL).

Pappostipa sect. **Chrysovaginatae** Romaschenko, sect. nov. TYPE: *Pappostipa chrysophylla* (E. Desv.) Romaschenko.

A *Pappostipa* sect. *Pappostipa* imis vaginis pallidis vel pauce aurantis (non rubro-fuscis) et imis foliis tenuis et fasciculatis, non coriaceis, setaceis (valde acutis, sed non pungentibus), verticalibus, convolutis (teretibus in trans-sectione), et cum non profundibus adaxialibus sulcis.

Pappostipa sect. *Chrysovaginatae* differs from *P.* sect. *Pappostipa* by having pale or stramineous to golden, basal sheaths and basal leaves that are thin and not coriaceous, setaceous (sharply pointed but not pungent), straight, convolute (terete in cross section), and with shallow adaxial furrows. All species have type II leaf anatomy as described by Arriaga (1983).

Pappostipa sorianoi (Parodi) Romaschenko, comb. nov. BASIONYM: *Stipa sorianoi* Parodi, Revista Argent. Agron. 27(3–4):94, f. 5, B, b–e. 1960. *Jarava sorianoi* (Parodi) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: ARGENTINA. SANTA CRUZ: 20 km al norte de Perito Moreno, 13 Dec 1954, *A. Soriano 4775* (HOLOTYPE: BAA!).

Pappostipa atacamensis (Parodi) Romaschenko, comb. nov. BASIONYM: *Stipa atacamensis* Parodi, Revista Argent. Agron. 27(3–4):85, f. 3. 1960 [1961]. *Jarava atacamensis* (Parodi) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: CHILE. ATACAMA: Depto. Copiapó, Quebrada de Plaza, 3600m, 4 Feb 1949, *A. Krapovickas & J. Hunziker 5789* (HOLOTYPE: BAA-2964; ISOTYPES: CONC-29647, SGO-73250).

Pappostipa nana (Speg.) Romaschenko, comb. nov. BASIONYM: *Stipa nana* Speg., Revista Argent. Bot. 1:23. 1925. *Jarava nana* (Speg.) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: ARGENTINA. SANTA CRUZ: 1/2 legua al S de la laguna de Sehuenaiken, 3 Feb 1903, *C. Spegazzini s.n.* (HOLOTYPE: LP ex LPS-2501).

Pappostipa ibarii (Phil.) Romaschenko, comb. nov. BASIONYM: *Stipa ibarii* Phil., Anales Univ. Chile 93:716. 1896. *Jarava ibarii* (Phil.) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: CHILE: Patagonia ad lacum Pinto, Dec 1877, *H. Ibar s.n.* (HOLOTYPE: SGO-45658; ISOTYPES: B, BAA-3092 fragm. ex B, SGO-62799, US-1762378 fragm. ex SGO!, US-141625 fragm!, US-photo ex SGO-45658!).

Pappostipa ibarii f. **pallescens** (Parodi) Romaschenko, comb. nov. BASIONYM: *Stipa ibarii* f. *pallescens* Parodi, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):55–57, t. 11. 1964. *Jarava ibarii* f. *pallescens* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA: Las Heras, Paramillo de Uspallata, entre 2600–2800m, 18–19 Feb 1938, *A. Ruiz Leal 4830* (HOLOTYPE: BAA).

Pappostipa ibarii var. **anomala** (Parodi) Romaschenko, comb. nov. BASIONYM: *Stipa ibarii* var. *anomala* Parodi, Revista Argent. Agron. 27(3–4):89. 1960. *Jarava ibarii* var. *anomala* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA. SANTA CRUZ: Depto. Río Chico, Gdor. Gregores, *A. Soriano 5080* (HOLOTYPE: BAA).

Pappostipa ameghinoi (Speg.) Romaschenko, comb. nov. BASIONYM: *Stipa ameghinoi* Speg., Anales Mus. Nac. Montevideo 4(2):163–165, f. 50. 1901. *Jarava ameghinoi* (Speg.) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: ARGENTINA. SANTA CRUZ: Golfo San Jorge, Aest. 1899, *C. Ameghino s.n.* (HOLOTYPE: LP-12593 ex LPS).

Pappostipa ameghinoi var. **digona** (Parodi) Romaschenko, comb. nov. BASIONYM: *Stipa ameghinoi* var. *digona* Parodi, Revista Argent. Agron. 27(3–4):80, f. 2. 1960. *Jarava ameghinoi* var. *digona* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA. SANTA CRUZ: Chicorikaike, 50° S 69° 25' W, Jan 1930, *A. Renard 13* (HOLOTYPE: BAA).

Pappostipa ameghinoi var. **precordillerana** (F.A. Roig) Romaschenko, comb. nov. BASIONYM: *Stipa ameghinoi* var. *precordillerana* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 12(1):79, 80–81, t. 1. 1965. *Jarava ameghinoi* var. *precordillerana*

(F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA. MENDOZA: Las Heras, Alto de los Manantiales, 20 Feb 1965, *F.A. Roig 5284* (HOLOTYPE: MERL; ISOTYPE: LP).

Pappostipa chubutensis (Speg.) Romaschenko, comb. nov. BASIONYM: *Stipa chubutensis* Speg., Anales Mus. Nac. Montevideo 4(2):49–51, f. 7. 1901. *Jarava chubutensis* (Speg.) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: ARGENTINA. CHUBUT: Teka Choque, Feb 1900, *O. Mauri s.n.* (HOLOTYPE: BAA ex LPS-2477; ISOTYPES: US-1721311!, US-141588!).

Pappostipa chubutensis var. **hirsutissima** (F.A. Roig) Romaschenko, comb. nov. BASIONYM: *Stipa chubutensis* var. *hirsutissima* F.A. Roig, Bol. Soc. Argent. Bot. 14(4):316, f. 3. 1972. *Jarava chubutensis* var. *hirsutissima* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA. SANTA CRUZ: Depto. Puerto Deseado, 30 km al S de Puerto Deseado por ruta 282, 20 Nov 1963, *Correa et al. 2638* (HOLOTYPE: BAA; ISOTYPES: BAA-BAB, LP).

Pappostipa frigida (Phil.) Romaschenko, comb. nov. BASIONYM: *Stipa frigida* Phil., Fl. Atacam. 54. 1860. *Jarava frigida* (Phil.) F. Rojas, Gayana, *Bot.* 54(2):173. 1997 [1998]. TYPE: CHILE: cerro Altos de Puquios, ca. 3810m, Feb. 1864, *Philippi s.n.* (HOLOTYPE: SGO-63153).

Pappostipa frigida var. **parvispicula** (Parodi) Romaschenko, comb. nov. BASIONYM: *Stipa frigida* var. *parvispicula* Parodi, Revista Argent. Agron. 27(3–4):91, f. 4, E, e. 1960. *Jarava frigida* var. *parvispicula* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA. LA RIOJA: Depto Sarmiento, Paso de Pircas Negras, 4100m, en el límite Argentino–Chileno, 6 Feb 1949, *A. Krapovickas & J. Hunziker 5798* (HOLOTYPE: BAA; ISOTYPES: BAB, CORD).

Pappostipa humilis (Cav.) Romaschenko, comb. nov. BASIONYM: *Stipa humilis* Cav., Icon. 5:41, t. 466, f. 1. 1799. *Jarava humilis* (Cav.) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: CHILE: Puerto Deseado, "Habitat in Americae meridionalis portu vulgo Deseado in solo arido, floretque Decembri, Luis Née s.n.," *Nee s.n.* (HOLOTYPE: MA; ISOTYPES: SGO photo, US-866105 fragm!).

Pappostipa humilis var. **decrescens** (Kuntze) Romaschenko, comb. nov. BASIONYM: *Stipa humilis* var. *decrescens* Kuntze, Revis. Gen. Pl. 3(3):371. 1898. *Jarava humilis* var. *decrescens* (Kuntze) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA: Patagonia, Paso Cruz, 2000m, 1 Apr 1882, *Moreno & Tonini 285* (SYNTYPE: NY!; ISOSYNTYPE: US-A866104 ex NY!).

Pappostipa humilis var. **ruiziana** (Parodi) Romaschenko, comb. nov. BASIONYM: *Stipa humilis* var. *ruiziana* Parodi, Revista Argent. Agron. 27(3–4):104. 1960. *Jarava humilis* var. *ruiziana* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA. MENDOZA: Depto. Las Heras, cerca de Hornillos, abundante, 21 Jan 1944, *A. Ruiz Leal 8593* (HOLOYPE: BAA).

Pappostipa chrysophylla (E. Desv.) Romaschenko, comb. nov. BASIONYM: *Stipa chrysophylla* E. Desv., Fl. Chil. 6:278, t. 76, f. 2. 1854. *Stipa humilis* f. *chrysophylla* (E. Desv.) Kuntze, Revis. Gen. Pl. 3(3):371. 1898. *Stipa speciosa* subsp. *chrysophylla* (E. Desv.) Dusén, Rep. Princeton Univ. Exp. Patagonia, Bot., Suppl. 8(3):30–31. 1914 [1915]. *Jarava chrysophylla* (E. Desv.) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: CHILE: Coquimbo, en el valle de Toro a 3497m, sobre un terreno de fonolito, y en el de los Patos, *C. Gay 376* (SYNTYPE: P; ISOSYNTYPE: US-866134!). CHILE: Habita en los helechos de los cordilleras altas de Guanta a 2003m, y también en Copiapó, *Gay s.n.* (SYNTYPE: ?).

Pappostipa chrysophylla f. **minuta** (F.A. Roig) Romaschenko, comb. nov. BASIONYM: *Stipa chrysophylla* f. *minuta* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):66, t. 25b. 1964 [1966]. *Jarava chrysophylla* f. *minuta* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA: Malalhue, Los Molles, 1850–1950m, césped pequeño, hojas erectas, 11–22 Feb 1960, *A. Ruiz Leal 20847* (HOLOTYPE: MERL?).

Pappostipa chrysophylla var. **cordillerarum** (Parodi) Romaschenko, comb. nov. BASIONYM: *Stipa chrysophylla* var. *cordillerarum* Parodi, Revista Argent. Agron. 27(3–4):99. 1960. *Jarava chrysophylla* var. *cordillerarum* (Parodi) Peñailillo, Gayana, Bot. 59(1):31. 2002. TYPE: ARGENTINA. LA RIOJA: Depto. Sarmiento, quebrada de las Cuevas, dominante en las laderas a 3900m, *A. Krapovickas & J. Hunziker 5855* (HOLOTYPE: BAA; ISOTYPE: CORD).

Pappostipa chrysophylla var. **crispula** (Kuntze) Romaschenko, comb. nov. BASIONYM: *Stipa humilis* f. *crispula* Kuntze, Revis. Gen. Pl. 3(3):371. 1898. *Stipa chrysophylla* var. *crispula* (Kuntze) Parodi, Revista Argent. Agron. 27(3–4):98. 1960. *Jarava chrysophylla* var. *crispula* (Kuntze) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA: Paso Cruz, Cordillera, 34°N, 1500m, 1 Jan 1892, *C.E.O. Kuntze 72* (HOLOTYPE: NY!).

Pappostipa chrysophylla f. **modica** (F.A. Roig) Romaschenko, comb. nov. BASIONYM: *Stipa chrysophylla* f. *modica* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):66–67. 1964 [1966]. *Jarava chrysophylla* f. *modica* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. TYPE: ARGENTINA: Las Heras, Paramillo de Uspallata, 2800m, 9–11 Feb 1964, *A. Ruiz Leal 23249* (HOLOTYPE: MERL?).

DISCUSSION

Basal lineages.—In order to focus on *Jarava* s.l. and the major American lineages of the Stipeae in the present paper we have excluded all except representatives of two extra-American lineages (i.e., one Asian *Ptilagrostis* and five species of the Australian genus *Austrostipa*) of Stipeae from our DNA analyses. Several small American genera were excluded from the present paper as they were not considered to be pertinent to the subjects of the present paper (see Methods), but they will be treated in subsequent publications. The phylogenetic patterns we detected with the present data are consistent with those detected with our larger worldwide dataset for Stipeae (preliminary ITS plastid analysis presented by Romaschenko et al. 2007; and

unpublished chloroplast DNA data). Because our taxon sampling here is purposefully curtailed, discussions of the basal radiations in the tribe are necessarily restrained in this paper. Since there is a larger phylogenetic story in the full dataset, not too much should be read into the placement of *Austrostipa* by itself as sister to the Major American Clade (MAC) in which, *Achnatherum*, *Jarava* s.s., *Nassella*, and *Amelichloa* are included. Nevertheless, some things can be said about the basal lineages as resolved here.

The early diverging or sister group position of the basal lineages (here *Piptochaetium*, *Ptilagrostis*, and *Anatherostipa*) in relation to *Achnatherum*, *Amelichloa*, *Austrostipa*, *Jarava* s.l., and *Nassella* [AAAJN] has never been indicated in previous reconstructions of the phylogeny of the Stipeae. An early diverging position of *Piptochaetium* (as a part of a complex of North American *Piptatherum/Oryzopsis* plus *Piptochaetium*) within Stipeae was reported by Jacobs et al. (2000) based on ITS sequence analysis. However, the authors assigned more weight to morphological similarities of this group with *Nassella* and consequently the early diverging position of *Piptochaetium* was thought to be an artifact. The early diverging position of *Piptochaetium* also was not recognized when a larger data set was used (Jacobs et al. 2007). Various morphological characters, such as: short, obovate floret, eccentric straight hairless awns, development of a crown, bulbous-based hairs on the apex of the lemma, silicified walls of fundamental cells of the lemma epidermis, and type of epiblast has suggested a close relationship between *Piptochaetium* and *Nassella* (Thomasson 1978; Barkworth & Everett 1987; Barkworth 1990, 1993; Jacobs et al. 2000; Barkworth & Torres 2001; Cialdella & Giussani 2002). In contrast to these conclusions, our data support a monophyletic origin of *Piptochaetium* near the base of the American Stipeae, thereby rendering *Nassella* and *Piptochaetium* as distant relatives. An independent origin of the above suite of characters in *Piptochaetium*, well removed from *Nassella*, is in agreement with the latest revision of *Piptochaetium* based on phylogenetic analysis of plastid *trn*L-F and *rpl*16 sequences and morphological characters (Cialdella et al. 2007).

All three genera of our "basal lineages" set (i.e.; *Piptochaetium*, *Ptilagrostis*, and *Anatherostipa*) have a "saw" like pattern on the lemma fundamental cells, where the side walls are usually much longer than end walls, strictly sinuate, lobate or dentate, and fundamental cells do not regularly alternate with silica cells (Barkworth 1983; Barkworth & Everett 1987). This lemma epidermal pattern is evidently the plesiomorphic condition in Stipeae and can be assumed to be an unspecialized characteristic within the Pooideae since no other pattern has been detected so far in mid to early fossil stipoid grasses (Thomasson 1978, 1980, 1981, 1982, 1985). There are unambiguously identifiable fossils from the Oligocene of the Stipeae called *Berriochloa* M.K. Elias with a "saw" like pattern in the lemma epidermis. Some early Pliocene fossils referred to *Nassella* (Thomasson 1978) have short fundamental cells but still have sinuate sidewalls and end walls like the basal lineages identified here, such as *Piptochaetium* but unlike extant species of *Nassella*.

Our molecular analyses indicate that *Ptilagrostis* and *Achnatherum* are also phylogenetically distant. This conclusion is further supported with micromorphological data, as the two genera have different lemma epidermal patterns (Barkworth 1983; Barkworth & Everett 1987). Based on the topology of our trees (Figs. 1–3), the polarization of the epidermal characters from *Achnatherum* (as a conditionally ancient state) to *Ptilagrostis* (as a conditionally derived state), as proposed Tzvelev (1977) and Barkworth and Everett (1987), is not parsimonious. We deduce that *Ptilagrostis* has the ancestral conditions for epidermal characters.

The monophyly of the genus *Anatherostipa* is supported by all our molecular analyses (Figs. 1–3) and *Ptilagrostis* appears to be the sister group of *Anatherostipa* plus *Piptochaetium* (Figs. 2 & 3). Key features of *Anatherostipa* other than the "saw" like lemma epidermal pattern, are the short glumes relative to the lemmas, long (often prow-tipped) paleas, and lemmas occasionally with small teeth or lobes at the apices (Matthei 1965; Barkworth & Everett 1987). These lemma apex characteristics were considered by Tzvelev (1977) to be an ancestral or plesiomorphic state in the Stipeae. Species of *Anatherostipa* share the lemma surface pattern and apical teeth character with *Ptilagrostis*.

The great variation in morphological forms, particularly the diversity of modifications in shape and size of floret and awn indumentum with apparent adaptive functions, within the basal lineages and MAC, is a primary reason why these separate groups were difficult to detect based solely on the study of mor-

phology. This confirms the suggestions of Thomasson (1978, 1985) and Barkworth and Everett (1987) that similar adaptive forms evolved independently, possibly synchronously under similar ecological pressures, in phylogenetically distant groups of Stipeae. Despite being morphologically diverse due to the anemochoric or herbivoric adaptations, in addition to sharing the unique lemma epidermal pattern, the basal lineages among themselves have relatively low levels of divergence in DNA sequences. The divergence value for the most variable ITS region was 17.6% for the out-group to ingroup taxa and is only 2.9% for the basal lineages. This latter value is not significantly higher than for *Nassella* where it was 2.6%. Relatively high (up to 4%) sequence divergence values between the basal lineages and the *Hesperostipa* clade indicates a greater evolutionary distance between them even though they share the "saw" like lemma pattern. The "saw" like lemma epidermal pattern found in the basal lineages is also known to occur in *Hesperostipa* (Thomasson 1978, 1980, 1982, 1985; Barkworth 1990; Cialdella & Giussani 2002). *Hesperostipa* also shares a long and prow-tipped palea with *Anatherostipa* (Barkworth & Everett 1987). *Hesperostipa* is a small phylogenetically and geographically isolated genus of the North American Stipeae.

Pappostipa.—The phylogenetic history of the *Pappostipa* clade supported by our molecular analysis of plastid DNA and nrDNA sequences (Figs. 1–3) provides evidence that *Jarava* s.l. is polyphyletic and the circumscription of the genus proposed by Peñailillo (2002) cannot be maintained. Consequently, we elevated all of Spegazzini's *Stipa* sect. *Pappostipa* to generic status based on corroborating morphological and anatomical evidence of differences with the remainder of *Jarava*. The phylogenetic resolution of *Austrostipa* and *Achnatherum* clades between *Pappostipa* clade and more highly derived *Jarava* s.s. clade clearly indicates that *Pappostipa* and *Jarava* s.s. do not share a most recent common ancestor. *Pappostipa* appears to be independently derived from the group we have called the Major American Clade (MAC). MAC is comprised of related genera that are geographically restricted to the Americas, with *Jarava* s.s. and *Nassella* constituting the principal part of the clade. Recent phylogenetic inferences based on plastid DNA sequences for the South American Stipeae (Cialdella et al. 2007) revealed the affinities of *Pappostipa* with the basal lineages since *Pappostipa vaginata* was inferred to be the sister group of an *Aciachne-Anatherostipa-Piptochaetium* clade. The phylogenetic position of *Pappostipa speciosa* (reported as "*Achnatherum speciosum*") within the *Achnatherum* clade based on ITS sequences by Jacobs et al. (2000, 2007) is refuted by our more extensive analysis.

Some key morphological features of the *Pappostipa* floret indicate transitional characteristics leading to the more advanced states found in MAC, or to analogous states of characteristics independently derived in other genera. Unigeniculate awns, straight and long-hairy columns, and usually straight glabrous bristles are the principal diagnostic characters for *Pappostipa* (Spegazzini 1901). The same suite of morphological features of the awn is developed in central Asian *Stipa* sect. *Pseudoptilagrostis* Tzvel. (Tzvelev 1977) and two Mediterranean genera, *Celtica* F.M. Vázquez & Barkworth and *Macrochloa* Kunth (Vázquez & Barkworth 2004). Among awn characteristics, *Ptilagrostis* differs from *Pappostipa* by having twice geniculate awns, and *Macrochloa* differs from *Pappostipa* by having falcate rather than straight bristles. The callus of *Pappostipa* is narrowly acute to acuminate with a characteristic lanceolate or linear-lanceolate form with a basally open foveola that follows the shape of the peripheral ring (Fig. 4A–C). However, a similar structure is known in *Stipa subsessiliflora* (Rupr.) Roshev. and *Stipa* sect. *Pseudoptilagrostis* (Freitag 1985; Barkworth & Everett 1987. After complete removal of the cuticle the walls of the lemma epidermal cells appear to be sinuate in *Pappostipa* (Fig. 4G) and not lobate. This type of lemma epidermal wall can be considered transitional between the "saw" like pattern found in *Hesperostipa* and other basal lineage genera (Fig. 4G) and the pattern found in MAC. However, the moderate shortening of the fundamental cells and their regular alternating pattern with equilateral silica cells ("maize" like pattern) enables us to associate the lemmas of *Pappostipa* with other achnatheroid type species rather than with the pattern encountered in the basal lineages.

Our ITS analysis and combined plastid DNA and nrDNA analyses (Figs. 2&3) divides *Pappostipa* into two clades that are correlated with anatomical types I & II of Arriaga (1983). These lineages are here named as *Pappostipa* sect. *Pappostipa* and *P.* sect. *Chysovaginatae*. Based on our molecular analyses and by possessing a suite of anatomical and leaf morphological characteristics we placed *Pappostipa barrancaensis*, *P. braun-*

blanquetii, P. hieronymusii, P. maeviae, P. major, P. malahuensis, P. nicorae, P. parodiana, P. patagonica, P. ruiz-lealii, P. speciosa, P. vaginata, and *P. vatroensis* in *P.* sect. *Pappostipa*; and include *P. ameghinoi, P. atacamensis, P. chrysophylla, P. chubutensis, P. frigida, P. humilis, P. ibarii*, and *P. nana* in *P.* sect. *Chysovaginatae*. Within *P.* sect. *Pappostipa* we also recognize an informal "long-bristle" group that includes *P. barrancancaensis, P. major, P. malahuensis*, and *P. vatroensis*. These four species all have long straight bristles, whereas the other species have "short bristles." We have recognized *P. speciosa* var. *major* as a species, *P. major*, based on different chromosome number reports (2*n*=60 in *P. major*; 2*n*=66 in *P. speciosa*; Parodi 1960; Stebbins & Löve 1941; Covas & Bocklet 1945), distinct differences in the length of the hairs on the lemma and glumes, thickness of the basal leaf blades, and color of the sheaths.

Austrostipa.—The monophyly of the Australian Stipeae, i.e., *Austrostipa* was supported in all of our separate and combined analyses of plastid DNA and nrDNA regions (Figs 1–3). The *Austrostipa* clade is clearly positioned as a sister group to the Major American Clade (MAC) composed of *Achnatherum, Jarava s.s.*, and *Nassella* (with *Amelichloa* nested inside). This general relationship, but with more Asian genera represented in the clade in which *Austrostipa* was included, was detected by Romaschenko et al. 2007. The monophyly of the *Austrostipa* was supported by Jacobs et al. (2000, 2007) based on the ITS analysis. However, the clade was thought to be the most derived group in the Stipeae, preceded by clades or grades containing *Nassella, Jarava,* and *Achnatherum*. It has been pointed out by Barkworth and Everett (1987) that the majority of the *Austrostipa* species do not have shortened fundamental cells, which is a distinctive character in species of *Nassella* and *Jarava* s.s. In addition, it was found that *Austrostipa* species typically have fundamental cells with slightly sinuate walls that sometimes are two or three times longer than the silica cells (Jacobs & Everett 1996). Therefore, we consider *Austrostipa* to be a somewhat specialized group and transitional to the American *Achnatherum*. However, the nature of this lineage will be covered in more detail in a separate paper where it will be placed in context of a World wide sample of the Stipeae.

Major American Clade.—One of the primary challenges of this study was to verify monophyly and ascertain the boundaries of the largest group of American Stipeae. We call it the Major American Clade (MAC) because it contains nearly 72% of the species in the American Stipeae. MAC appears to be monophyletic and is a geographically distinct lineage comprised of *Achnatherum* (American lineage), *Jarava* s.s. (as a clade or grade), *Amelichloa*, and *Nassella*. MAC has consistent statistical support (Figs. 1–3) as a lineage and appears as a sister group to *Austrostipa*. The detection of MAC provides a new phylogenetic hypothesis for the evolutionary derivation of the majority of the American Stipeae.

Achnatherum.—The monophyly of the subset American species of *Achnatherum* sampled (4 out of 34 species) was supported by our plastid and nuclear-derived trees (Figs. 1–3) and this *Achnatherum* clade was always the sister group to the *Jarava* s.s. plus the *Nassella-Amelichloa* complex, in agreement with analyses by Jacobs et al. (2000). Jacobs et al. (2000) suggested that *Achnatherum* was a close relative of *Austrostipa*, a hypothesis that is also supported by our analysis. *Achnatherum* clearly exhibits a derived lemma epidermal pattern (with fundamental cells that alternate with silica cells forming a clear "maize" pattern), and does not have the "saw" like lemma epidermal pattern found in the basal lineages and *Hesperostipa*.

Jarava s.s-Nassella complex.—The core of MAC is the *Jarava s.s.* plus *Nassella-Amelichloa* complex. This group contains ca. 160 species, representing about 60% of the American Stipeae. In all combined analyses of plastid DNA and nrDNA this clade was resolved as monophyletic with high statistical support (Figs. 1–3). Jacobs et al. (2000, 2007) did not detect this complex as a clade in their ITS tree, whereas recent phylogenetic inferences based on plastid DNA data (Cialdella et al. 2007) are consistent with our results. However, topologies yielded by parsimony and Bayesian analyses were not consistent when using separate data sets of plastid and nuclear markers. Based on combined data of plastid DNA regions, *Jarava plumosula* was placed in a polytomy between the *Nassella-Amelichloa* clade and the core of *Jarava* s.s. clade. *Jarava* s.s was resolved as monophyletic only in combined analysis of all genetic markers (Fig. 3).

Morphologically, the *Jarava* s.s. plus *Nassella-Amelichloa* complex exhibits short paleas and short funda-

mental cells. These traits are most highly developed in *Nassella* where species are characterized by having a "ladder" pattern of the lemma epidermal cells, designated by Barkworth (1990) as the "nasselloid type" (short, silicified fundamental cells not alternating with silica cells, or fundamental cells and short cells that lack silica) that are indistinguishable from each other. Another distinct feature of species with nasselloid type lemma anatomy is the development of the crown (a fleshy, ciliate formation) at the apex of the lemma. Species of *Jarava* s.s. are characterized here as the "achnatheroid type," with fundamental cells that alternate with silica cells of the same form (Fig. 4H), forming a clear "maize" pattern, and with the absence of a lemma crown. Among other achnatheroid traits common for *Jarava* s.s. species, but not observed in *Nassella* or *Amelichloa,* are the protruding and/or in some cases reduced, lemma lobes.

***Jarava* s.s.**—Based on our current set of samples, as seen in Figs. 2&3, the *Jarava* s.s. clade consists of two distinct groups: 1) *Jarava ichu* group; and 2) *J. plumosula* group. In the ITS analysis, the *Jarava* s.s. clade was resolved to be polyphyletic, with three species constituting *J. plumosula* group forming a clade that is sister group to *Nassella-Amelichloa* (Fig. 2). In the plastid analysis (Fig. 1) only *J. plumosula* resolved in a polytomy between the core of *Jarava* and *Nassella-Amelichloa*, whereas *J. media* and *J. polyclada* were placed just at the base of the clade of *Jarava* s.s. (core) plus *Nassella-Ameichloa* complex. In the analysis of the whole molecular dataset, all species of *Jarava* s.s. were weakly supported as monophyletic clade (Fig. 3). *Jarava media, J. plumosula*, and *J. polyclada* all share the same habitat and a habit that includes such characters as culms having many branches at the upper nodes, and a zoo-anemochoric floret dispersal adaptations.

Our combined plastid and ITS molecular analysis (Fig. 3) supports the separation of *Jarava leptostachya* from species formerly recognized as *Stipa capilliseta* Hitchc. [≡ *S. leptostachya* var. *capilliseta* (Hitchc.) Parodi, currently treated as a synonym of *J. leptostachya* in Soreng et al. 2003] and consequently, labeled on the trees as *J. leptostachya*[2]. This separation is supported by morphological differences such as, a flexuous awn and sparsely hairy lemma apices in *S. capilliseta* verses a geniculate awn and pappose lemma apices in *J. leptostachya*.

Nassella including Amelichloa.—According to the latest revision, *Nassella* is one of the largest genera in the tribe (Barkworth & Torres 2001) with some 119 species listed as accepted by Soreng et al. (2003). A number of subgeneric and sectional names were employed in *Stipa* s.l. by Spegazzini (1901, 1925) and Roig (1964) to recognize the many forms now placed in *Nassella*. Despite some striking morphological differences among the species, the majority of the species of *Nassella* share the same "nasselloid" pattern of the floret defined by Barkworth (1990). This pattern includes short paleas, strongly overlapping lemma margins, presence of crown, and a unique lemma epidermal pattern. Our nuclear and combined plastid-nuclear consensus trees yielded a *Nassella-Amelichloa* clade with high statistical support (Figs 2 & 3). The internal structure within our *Nassella-Amelichloa* clade is represented by two well-supported branches accommodating groups of species of varying morphological homogeneity. Within *Nassella*, the upper clade of Figs. 2 & 3 (incl. *N. brachychaetoides, N. brachyphylla, N. caespitosa, N. dasycarpa, N. depauperata, N. inconspicua, N. meyeniana, N. nardoides, N. pubiflora,* and *N. rupestris*) shares similar morphological features as described for *Stipa* subg. *Dasystipa* Speg. by Spegazzini (1901). This group typically has: oblong or lanceolate, often truncate florets, hairy lemmas (sometimes the hairs are much longer at the apex of the lemma), eccentric marginiform crowns (rarely inconspicuous), and florets with a short callus. The lower clade within *Nassella* (Figs. 2&3) includes *Amelichloa* (*A. caudata* and *A. clandestina*) and taxa attributed to *Stipa* subg. *Stephanostipa* Speg. (incl. *N. clarazii, N. filiculmis, N. manicata, N. neesiana, N. nidulans, N. pfisteri,* and *N. rosengurttii*), *Stipa* subg. *Nassella* (*N. trichotoma, N. tenuissima and N. sanluisensis* sensu Spegazzini 1901), and *Stipa* subg. *Microstipa* (incl. *N. filiculmis* sensu Spegazzini 1901; and *N. tenuissima* sensu Roig 1964). In combined plastid DNA-nrDNA and ITS analyses the *Amelichloa* subclade was resolved as monophyletic (PP=1.00; BF=100) as a sister group to the lower clade of *Nassella*. The position of the *Amelichloa* clade near the base of this lower *Nassella* clade was unexpected. However, all species of *Nassella-Amelichloa* share a deletion of three nucleotides at the end of the ITS-2 region (not coded for this analysis) not found in other taxa of our analysis. The position of *Amelichloa* within *Nassella* requires study of additional species prior to proposing taxonomic changes.

CONCLUSIONS

Jarava s.l. is polyphyletic and species formerly in *Stipa* subg. *Pappostippa* are removed from *Jarava* s.l. and placed in the new genus *Pappostipa*. This new genus is phylogenetically intermediate between a group of genera designated as the basal lineages in the American Stipeae and a set of genera designated here as the Major American Clade. The Major American Clade includes: *Achnatherum* of the New World, *Jarava* s.s., and *Nassella* (in which the genus *Amelichloa* is phylogenetically nested). The American basal lineages include a clade of *Anatherostipa* and *Piptochaetium* as sister group to the Asian and American genus *Ptilagrostis*. Phylogenetically, the North American genus *Hesperostipa* stands between these American basal lineages and *Pappostipa* plus the Major American Clade.

ACKNOWLEDGMENTS

We wish to thank the following organizations or persons: the Fulbright Scholar Program to KR for a research visit to the Smithsonian Institution; the Smithsonian Institutions, Restricted Endowment Fund, the Scholarly Studies Program, Research Opportunities, Atherton Seidell Foundation, and Biodiversity Surveys, Inventories Program, and Laboratory of Analytical Biology for financial support and excellent research facilities; Lee Weigt, Jeffrey Hunt, David Erickson, Kenneth Wurdack, and Andrea Ormon for support and consultation; Roser Villatersana, Teresa Garnatje, and Oriane Hidalgo for help in the laboratory; Asuncion Cano Echevarría, Oscar Tovar Serpa, Dorita Susanibar Cruz, Socorro González Elizondo, Nancy Refulio Rodríguez, Fernando Zuloaga, and Stephan Beck for help with our recent field expeditions to Peru, Bolivia, and Argentina; Samuel Pyke for providing samples; Pedro Acevedo Rodríguez for help with the Spanish resumen; Alain Touwaide for help with the Latin diagnosis; and Jeff Saarela and Emmet Judziewicz for providing helpful comments on the manuscript.

REFERENCES

Arriaga, M.O. 1983. Anatomia foliar de las especies de *Stipa* del subgenero *Pappostipa* (Stipeae-Poacecae) de Argentina. Revista Mus. Argent. Ci. Nat., Bernardino Rivadavia Inst. Nac. Invest. Ci. Nat., Bot. 6(4):11–41.

Arriaga, M.O. and M.E. Barkworth. 2006. *Amelichloa*, a new genus in the Stipeae (Poaceae). Sida 22:145–149.

Barkworth, M.E. 1983. *Ptilagrostis* in North America and its relationship to other Stipeae (Gramineae). Syst. Bot. 8:395–419.

Barkworth, M.E. and J. Everett. 1987. Evolution in Stipeae: identification and relationship of its monophyletic taxa. In: T.R. Soderstrom, K.W. Hilu, C.S. Campbell, and M.E. Barkworth, eds. Grass systematics and evolution. Washington, D.C. Pp. 251–264.

Barkworth, M.E. 1990. *Nassella* (Gramineae, Stipeae): revised interpretation and nomenclatural changes. Taxon 39:597–614.

Barkworth, M.E. 1993. North American Stipeae (Gramineae): taxonomic changes and other comments. Phytologia 74:1–25.

Barkworth, M.E. and M.A. Torres. 2001. Distribution and diagnostic characters of *Nassella* (Poaceae: Stipeae). Taxon 50:439–468.

Caro, J.A. and E. Sánchez. 1973. Las especies de *Stipa* (Gramineae) del subgénero *Jarava*. Kurtziana 7:61–116.

Cialdella, A.M. and L.M. Giussani. 2002. Phylogenetic relationships of the genus *Piptochaetium* (Poaceae, Pooideae, Stipeae): evidence from morphological data. Ann. Missouri Bot. Gard. 89:305–336.

Cialdella, A.M., L.M. Giussani, L. Aagesen, F.O. Zuloaga, and O. Morrone. 2007. A phylogeny of *Piptochaetium* (Poaceae: Pooideae: Stipeae) and related genera based on a combined analysis including *trn*L-F, *rpl*16, and morphology. Syst. Bot. 32:545–559.

Covas, G. and M. Bocklet. 1945. Número de cromosomas de algunas Gramineae–Stipinae de la flora Argentina. Revista Argent. Agron. 12:261–265.

Davis, J. I. and R.J. Soreng. 2007. A preliminary phylogenetic analysis of the grass subfamily Pooideae (Poaceae), with attention to structural features of the plastid and nuclear genomes, including an intron loss in GBSSI. Aliso 23:335–348.

Doyle, J.J. and J.L. Doyle. 1987. A rapid isolation procedure for small quantities of fresh tissue. Phytochem. Bull. Bot. Soc. Amer. 19:11–15.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using bootstrap. Evolution 39:783–791.

Freitag, H. 1985. The genus *Stipa* (Gramineae) in Southwest and South Asia. Notes Roy. Bot. Gard. Edinburgh 42:355–489.

Grass Phylogeny Working Group (GPWG). 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). Ann. Missouri Bot. Gard. 88:373–457.

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl. Acids. Symp. Ser. 41:95–98.

Hilu, K.W., A.A. Lawrence, and H. Liang. 1999. Phylogeny of *Poaceae* inferred from *mat*K sequences. Ann. Missouri Bot. Gard. 86:835–851.

Hitchcock, A.S. 1935. 96. *Stipa, Oryzopsis,* and *Piptochaetium*. N. Amer. Fl. 17:406–431.

Hitchcock, A.S. 1951. Manual of grasses of the United States (ed. 2, revised by A. Chase). U.S. Department of Agriculture Misc. Publ. 200:1–1051.

Huelsenbeck, J.P. and F.R. Ronquist. 2001. MrBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

Jacobs, S.W.L., R. Bayer, J. Everett, M. Arriaga, M. Barkworth, A. Sabin-Badereau, A. Torres, F. Vázquez, and N. Bagnall. 2007. Systematics of the tribe Stipeae (Gramineae) using molecular data. Aliso 23:349–361.

Jacobs, S.W.L. and J. Everett, J. 1996. *Austrostipa*, a new genus, and new names for Australian species formerly included in *Stipa* (Gramineae). Telopea 6:579–595.

Jacobs, S.W.L., J. Everett, and M.E. Barkworth. 1995. Clarification of morphological terms used in *Stipeae* (*Gramineae*) and a reassessment of *Nassella* in Australia. Taxon 44:33–41.

Jacobs, S.W.L., J. Everett, M.E. Barkworth, and C. Hsiao. 2000. Phylogenetic relationship within the *Stipeae*. Pp. 75–82. In: S.W.L. Jacobs and J. Everett, eds. Grasses: systematics and evolution. Collingswood, Australia.

Johnson, L.A. and D.E. Soltis. 1995. Phylogenetic inference in Saxifragaceae sensu stricto and *Gilia* (Polemoniaceae) using *mat*K sequences. Ann. Missouri Bot. Gard. 82:149–175.

Kress, W.J., K.J. Wurdack, E.A. Zimmer, L.A. Weigt, and D.H. Janzen. 2005. Use of DNA barcodes to identify flowering plants. Proc. Natl. Acad. U.S.A. 102:8369–8374.

Kuntze, O. 1898. Revis. Gen. Pl. 3(2) & 3(3):1–384. Arthur Felix, Leipzig.

Matthei, O.R. 1965. Estudio crítico de las gramíneas del género *Stipa* en Chile. Gayana, Bot. 13:1–137.

Nixon, K.C. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. Cladistics 15:407–414.

Nicora, E.G. and Z. Rúgolo de Agrazar. 1978. Gramineae. In: M.N. Correa, ed. Flora Patagónica. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires 3:1–563.

Nylander, J. A. 2002. MrModeltest v.1.1b. Program distributed by the author. Department of Systematic Zoology, Uppsala University, Uppsala.

Parodi, L.R. 1946. The Andean species of the genus *Stipa* allied to *Stipa obtusa*. Blumea 3:63–70.

Parodi, L.R. 1947. Las especies de Gramíneas del género *Nassella* de la Argentina y Chile. Darwiniana 7:369–395.

Parodi, L.R. 1960. Las especies de *Stipa* del subgénero *Pappostipa* de la Argentina y Chile. Revista Argen. Agron. 27(3–4):65–106.

Peñailillo, P. 1996. *Anatherostipa*, un nuevo género de *Poaceae* (Stipeae). Gayana, Bot. 53: 277–284.

Peñailillo, P. 2002. El género *Jarava* Ruiz et Pav. (Stipeae-Poaceae): delimitación y nuevas combinaciones. Gayana, Bot. 59:27–34.

Peñailillo, P. 2003. *Jarava* Ruiz et Pav pp. In: R.J. Soreng, P.M. Peterson, G. Davidse, E.J. Judziewicz, F.O. Zuloaga, T.S. Filgueiras, and O. Morrone, eds. Catalogue of New World grasses (Poaceae): IV. subfamily Pooideae. Contr. U.S. Natl. Herb. 48: 402-409.

Roig, F.A. 1964. Las Gramíneas mendocinas del género *Stipa*. I. Taxonomía. Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11:3–110.

Rojas P. F. 1997 [printed 1998]. Nuevas especies y nuevas combinaciones para la tribu *Stipeae* (Poaceae) en Bolivia. Gayana, Bot. 54:163–182.

Romaschenko, K., P.M. Peterson, N. Garcia-Jacas, R.J. Soreng, and A. Susanna. 2007. A Phylogeny of *Stipeae* (*Poaceae*) based on nuclear DNA (ITS) sequence data. Plant Biology and Botany 2007, Joint Congress, Chicago, USA http://bsa2007.scientific-conference.net/engine/search/index.php?func= detail&aid=2734

Ronquist, F., J.P. Huelsenbeck, and P. van der Mark. 2005. MrBayes 3.1 manual, draft 5/26/2005. http://mrbayes.csit.fsu.edu/mb3.1_manual.pdf

Sang, T., D.J. Crawford, and T.F. Stuessy. 1997. Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). Amer. J. Bot. 84:1120–1136.

Sikes, D.S. and P.O. Lewis. 2001. Beta software, version 1. PAUPRat: PAUP* implementation of the parsimony ratchet. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, USA.

Soltis, P.S. and D.E. Soltis. 2003. Applying the bootstrap in phylogeny reconstruction. Stat. Sci. 18:256–267.

Soreng, R.J. and J.I. Davis. 2000. Phylogenetic structure in *Poaceae* subfamily *Pooideae* as inferred from molecular and morphological characters: misclassification versus reticulation. In: S.W.L. Jacobs and J.E. Everett, eds. Grasses: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia. Pp. 61–74.

Soreng, R. J. and J.I. Davis. 2005. Phylogenetic structure of Poaceae subfamily Pooideae based on sequence data of five chloroplast-encoded genes: some biogeographic implications. XVII International Botanical Congress (IBC), Vienna, Austria. Abstract: http://www.ibc2005.ac.at/program/abstracts/IBC2005_Abstracts.pdf

Soreng, R.J., J.I. Davis, and M.A. Voionmaa. 2007. A phylogenetic analysis of *Poaceae* sensu lato based on morphological characters and sequence data from three plastid-encoded genes: evidence for reticulation, and new classification for the tribe. Kew Bulletin 62:425–454.

Soreng, R.J., P.M. Peterson, G. Davidse, E.J. Judziewicz, F.O. Zuloaga, T.S. Filgueiras, and O. Morrone. 2003. Catalogue of New World grasses (Poaceae): IV. subfamily Pooideae. Contr. U.S. Natl. Herb. 48:1–730.

Soreng, R.J., P.M. Peterson, G. Davidse, E.J. Judziewicz, F.O. Zuloaga, T.S. Filgueiras, and O. Morrone. 2008. Catalogue of New World grasses. http://mobot.mobot.org/W3T/Search/nwgc.html#Search updated 11 Jan 2008.

Spegazzini, C. 1901. Stipeae platenses. Anales Mus. Nac. Montevideo 4(2):1–173.

Spegazzini, C. 1925. Stipeae platenses novae v. criticae. Revista Argent. Bot. 1:9–51.

Stebbins, G.L. and R.M. Löve. 1941. A cytological study of California forage grasses. Amer. J. Bot. 28:371–382.

Stanford, A.M., R. Harden, and C.R. Parks. 2000. Phylogeny and biogeography of *Juglans* (Juglandaceae) based on *mat*K and ITS sequence data. Amer. J. Bot. 87:872–882.

Swofford, D.L. 2000. PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4. Sinauer Associates Inc., Sunderland, MA.

Taberlet, P., L. Gielly, G. Pautou, and J. Bouvet. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. Plant Molecular Biology 17:1105–1109.

Tate, J.A. and B.B. Simpson. 2003. Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploidy species. Syst. Bot. 28:723–737.

Thomasson, J.R. 1978. Epidermal patterns of the lemma in some fossil and living grasses and their phylogenetic significance. Science 199:975–977.

Thomasson, J.R. 1980. Paleoeriocoma (Gramineae, Stipeae) from the Miocene of Nebraska: taxonomic and phylogenetic significance. Syst. Bot. 5:233–240.

Thomasson, J.R. 1981. Micromorphology of the lemma in *Stipa robusta* and *Stipa viridula* (Gramineae: Stipeae): taxonomic significance. Southw. Naturalist 26:211–214.

Thomasson, J.R. 1982. Fossil grass anthoecia and other plant fossils from arthropod burrows in the Miocene of Western Nebraska. Journal of Paleontology 56:1011–1017.

Thomasson, J.R. 1985. Miocene fossil grasses: possible adaptation in reproductive bracts (lemma and palea). Ann. Missouri Bot. Gard. 72:843–851.

Tzvelev, N.N. 1977. [On the origin and evolution of Feathergrasses (*Stipa* L.)] In: Problemy ekologii, geobotaniki, botanicheskoi geografii i floristiki. Academiya Nauk SSSR, Leningrad. Pp. 139–150.

Vázquez, F.M. and M.E. Barkworth. 2004. Resurrection and emendation of *Macrochloa* (Gramineae: Stipeae). Bot. J. Linn. Soc. 144:483–495.

White, T.J., T. Bruns, S. Lee, and J. Taylor. 1990. Amplifications and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: M. Innis, D. Gelfand, J. Sninsky, and T. White, eds. PCR protocols: a guide to methods and applications. Academic Press, San Diego, California, USA. Pp. 315–322.

Zharkikh, A. 1994. Estimation of evolutionary distances between nucleotide sequences. J. Molec. Evol. 39:315–329.